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ELMER DREW MERRILL 1876-1956

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*With portrait \**

PROFESSOR ELMER DREW MERRILL, Arnold Professor of Botany, *emeritus*, and former director of the Arnold Arboretum, died on FEBRUARY 25, 1956, in the Lemuel Shattuck Hospital, Forest Hills, Massachusetts. Few American botanists were as well known or as widely honored as Dr. Merrill. Few, also, have published as much as he in his long and distinguished career as botanical administrator and research taxonomist. In a knowledge of the flora of Asia no one has equalled him and it is improbable that any future botanist can match his publications on the flora of that area.

Physically a man of slight build, Dr. Merrill's health was excellent and he often stated he never knew sickness until a short while after his retirement when he suffered the first of many strokes which were to cause his death. In early September of 1955 a severe attack ended his active career and caused him to be bedridden and paralyzed until his death five months later.

Many complete biographical sketches of Dr. Merrill have been published and in 1953 he published in the Asa Gray Bulletin the first part of his autobiographical memoirs with the promise of completion in later issues. Who's Who in America, American Men of Science and "Merrilliana," a volume of selections from his general writings which was published in his honor as a double number of *Chronica Botanica*, detail his career and his publications.

Elmer Merrill was born in East Auburn, Maine, in 1876. He entered the University of Maine in 1894 and an interest in biology supplemented by summer employment in the State Fish Hatchery replaced an earlier interest in engineering. He reports that his first collections of plant materials were inspired by Professor F. L. Harvey and that during his college career he amassed a collection of more than 2000 named specimens of all groups of plants which later were presented to the New England Botanical Club. Duplicates of these specimens were sent to the New York Botanical

\* This portrait was taken in 1950 by Dr. Louis O. Williams in Honduras.

Garden in exchange for a copy of Britton and Brown's *Illustrated Flora of the Northern United States* and through these specimens an early contact with N. L. Britton was established. Following his graduation Merrill returned to the University of Maine as an assistant in natural sciences where, although no formal postgraduate work was offered, he "rounded out his college work," "gained additional experience" and followed his own "inclinations in the pursuit of systematic botany, although having little or no supervision." For these efforts Dr. Merrill was awarded an M.S. degree by the university in 1904, although he states "I can hardly claim that it was an earned degree." In later life Dr. Merrill was similarly rewarded for his accomplishments when he received honorary degrees of Doctor of Science (University of Maine, 1926, and Harvard University, 1936) and Doctor of Letters (University of California, 1936, and Yale University, 1951).

From 1899 until 1902 Merrill worked for the U. S. Department of Agriculture as assistant agrostologist, serving part of this time as assistant to F. Lamson-Scribner. Apparently none to satisfied with his chosen employment, he entered the Medical School of George Washington University, but during the first semester of his second year was offered a position as botanist with the Insular Bureau of Agriculture in the Philippines. His spartan boyhood stood him in good stead for the active career which followed, for his acceptance of this position and his arrival in Manila in 1902 marked the start of over fifty years of devoted study of Oriental flora. In the Philippines Merrill observed that the Bureau of Forestry was in greater need of the services of a botanist than was the Bureau of Agriculture and within a few months of his arrival in Manila he obtained a joint appointment to both bureaus. Thereafter he devoted his time to a study of the plant materials of the archipelago, spending approximately half of his time in the field collecting. Few government officials of his period and certainly only a few botanists since that time have visited as many parts of the islands as did Dr. Merrill. Identification of the specimens collected proved impossible with the library resources at hand and so over a period of years a remarkable library was built up under his guidance. To Merrill also must go the credit for starting the herbarium collections in 1902 which, by 1922, two years before the end of his Philippine service, numbered 275,000 mounted specimens. Merrill lived to see both this magnificent herbarium and library destroyed by the Japanese during World War II and lent his unfailing assistance in securing duplicate books and specimens to rebuild this collection.

Merrill states that on reaching Manila his ambition was the preparation and publication of a general flora of the Philippines. However, the number of plants known from the Philippines as recorded in published literature was 2500 in 1900 when Merrill started collecting and over 14,000 in 1923 when the team with which he worked, Copeland, Whiteford, Elmer and others, had completed their intensive collecting. Identifications were made first by trips to the garden and the botanical institution at Buitenzorg and later, during his periodic leaves, in the principal herbaria of Europe. In



view of the difficulties of identification and of handling such a complex flora, it is not surprising that Merrill's original ambition of a general flora was never accomplished. He laid the groundwork for such a flora, however, and through his efforts we have today a "Flora of Manila," published in 1914 and "An Enumeration of Philippine Flowering Plants," published in sections between 1923 and 1926, the latter with a total of 2143 pages. Professor Merrill's personal copy of his Enumerations (now in the library of the New York Botanical Garden) was carefully annotated with new records, changes in nomenclature and additional bibliography. As he worked with the flora of the Philippines and was exposed to flora of other island and mainland areas in Asia, Dr. Merrill recognized that a larger approach was needed for a proper interpretation and definition of the many species in the Philippines. Thus his interests, while still in the Philippines, spread to the phytogeography of the area, as well as the flora of China, Borneo and Guam as indicated in his published papers.

As his seniority in the Philippines increased and his abilities were recognized, Dr. Merrill was called upon for other duties. His knowledge was needed at the young University of the Philippines where he had an appointment as associate professor and later, head of the Department of Botany, in spite of a teaching load of eighteen to thirty-six hours a week. At the Bureau of Science during the absence of the director he served as acting director and in 1919 he became the director, serving in this capacity until 1923. In his autobiography Dr. Merrill describes fully his frustration at the heavy administrative load, which was unsought, and also noted his resentment of the tasks which conflicted with his real desires for taxonomic botanical work. His efforts as director of the Bureau of Science, supervising the research activities in fields other than botany, enhanced his background in agriculture administration and prepared him for the offer received in 1923 to become dean of the College of Agriculture at the University of California. His decision to leave the Philippines was apparently based on several factors; the lack of any degree of permanence or of retirement benefits in his positions, increasingly demanding administrative duties and the separation from his family. Merrill had married in Manila in 1907 and four children were born of this marriage, three in the Philippines and one in Washington, D. C. The Merrills' second son died in the second month of his life and thereafter Mrs. Merrill and the children lived in the United States while Dr. Merrill remained in the Philippines. One such separation lasted five years.

In 1924 he left the Philippines to embark upon a career which was to have a remarkable influence on American botany when he accepted the position as dean of the College of Agriculture. In his autobiography Merrill describes the magnitude of the task he had undertaken. He was in charge of a faculty of three hundred and fifty individuals, but knew only one or two members personally. He "succeeded an administrator whose policies, to a considerable degree, had failed." "Reorganization and the rebuilding of the *esprit de corps* of the staff was essential. The institution was over-staffed in relation to its material equipment." The staff was divided

physically as well as intellectually. The solution of these problems was made easier in 1924 when Merrill was appointed director of the Agriculture Experiment Station, as well, and in this joint appointment his recommendations for reorganization of the faculties, research program and physical resources were possible. Merrill spent six years in these positions and his success in the reorganization can be summarized in his own words and those of his successor. In his autobiography Merrill reports:

"I had met with a certain degree of success in my administrative work . . . and had the confidence of the agricultural community, the leaders in agriculture, the staff of the College of Agriculture and of the administration and staff of the University. I had been brought to California to consummate certain definite things and these had, to a high degree, been accomplished. The perplexing problems of the institution had to a large degree been settled; policies had been established which met with the very general support of the industry and the institution. The staff had been increased; the material equipment very greatly enlarged; the annual budget augmented (from \$1,800,000 to \$2,500,000). Important new buildings had been provided for the University farm on the Berkeley campus and at Riverside."

His successor at California wrote an appreciation of Merrill which was published in the *California Countryman* and stated:

"His quickness of perception, his unfailing patience and courtesy, his great store of common sense, his promptness in taking action, his approachableness and consideration for others have won for him the admiration and high esteem of his colleagues. . . . We of the University of California record not only our deep regret at losing him but also our profound appreciation of his remarkable contribution to the success and effectiveness of the program of the College of Agriculture of the scientific activity of the University in general, of our gratitude for the friendship and sympathy which he has shown his colleagues unfailingly and of the high regard we all entertain for him as a scholar, a scientist and above all a lovable human being."

In underlining his many accomplishments Hutchison refers particularly to the fact that Merrill was instrumental in establishing one of the best sets of curricula for colleges of agriculture and that he encouraged and stimulated in a sympathetic manner the prosecution of research on fundamental problems which underlie the science of agriculture.

Merrill's several reports as director of the Agriculture and Experiment Station and as head of the College of Agriculture tell little of his scientific work. Instead they dwell on the administrative problems of morale, growth, physical resources and financial requirements so familiar in such reports. Even during these years of heavy administrative and academic responsibility, Merrill's research and publications on the flora of the Philippines, China and Asia in general did not lag. As he states in his autobiography:

"I devoted all my spare time to actual work in systematic botany and in building up the oriental reference herbarium of the University. This work was all done outside of office hours and some idea of its extent may be gained by the



statement that in these exceedingly busy six years I added in excess of 110,000 mounted specimens to the University herbarium; in this time also I prepared and published one volume of 316 pages on the flora of Borneo and numerous shorter papers on the plants of China, Borneo and the Philippines. This work in systematic botany was indeed my safety valve, for once in the herbarium, whether early in the morning before my office opened, at noon, after office hours or on Sundays or holidays, I immediately forgot my administrative problems and during these many hours devoted to botany, became merely a botanist interested in botanical matters only. At such times I never concerned myself with the numerous pressing problems of the Dean of Agriculture."

It was also during this period that herbarium work allowed the formulation in Merrill's mind of aids and improvements to the techniques used. The early developments of his innovations of cardboard herbarium boxes, literature clippings, detailed field labels and arrangement of specimens from the Orient by related geographic areas date from his years at California.

In 1926 a movement was initiated to establish a botanical garden in Los Angeles and Merrill, originally a member of the Garden Foundation, the holding corporation, also served as its first and apparently only director. The California Botanic Garden at Los Angeles, some four hundred miles away from the College of Agriculture, occupied a considerable portion of Merrill's time, for in 1927 and 1928 he was officially spending four-fifths and one-half of his time, respectively, in this position. The garden was destined to last but a few years, for the economic crash and depression, as well as Merrill's transfer to the New York Botanic Garden, spelled the end to this garden of eight hundred acres. Actually it was an active garden, however, during Merrill's supervision, for an administration building and greenhouses were built, and approximately twelve hundred species of plants were growing in various sections. Established seed and plant exchanges, foreign and domestic, were recorded and a young library was started. Most indicative of Merrill's hand, however, is the fact that in its brief existence the California Botanic Garden amassed an herbarium of 180,000 mounted specimens which, upon dissolution of the Garden, were transferred to the University of California at Los Angeles.

Merrill was approached in 1927 by officials of the Board of Managers of the New York Botanical Garden to determine whether he would be interested in becoming director of the latter organization following the retirement of Dr. N. L. Britton. In July of 1929 the matter came to definite form when the Board of Managers of the New York Botanical Garden held a special meeting to accept the resignation of Dr. Britton and Merrill reports that he learned of his appointment subject to his acceptance from an Associated Press dispatch in the San Francisco Chronicle. He also writes of personal family reasons for the change he was to undertake and comments, "If one were looking merely for power, one would not make the change, for the administration of an annual budget of \$2,500,000 in a dynamic and rapidly expanding institution was in sharp contrast to the administration of less than one-fifth of that amount in an institution that had

become almost static." The move apparently was not without regrets, for writing in 1930 from New York Merrill states:

"History repeats itself, in that frequently I have questioned my judgement in accepting my present position. As in California during my first year or two there I looked back to Manila with keen regrets that I had ever left that city, so I frequently look back to the University of California and wonder why I ever left such a dynamic, progressive, expanding institution to cast my lot with an institution that was practically static, very badly under-financed and more or less under fire for its past policies and accomplishments. To rebuild the *esprit de corps* of the staff of one institution with reasonably ample and increasing financial resources is one thing; to attempt the same thing in another institution with totally inadequate financial support and little prospect of its increase is another."

Merrill's move from the University of California to the New York Botanic Garden took place at the start of the long economic depression of 1929-1934. Perhaps his laments of 1930 as well as his actual decision to move are involved in the financial adjustments necessary in both organizations. The New York Botanic Garden was supported by funds from private endowment and in part by financial support of the city of New York. The University of California, in particular the College of Agriculture, depended on state aid. It is interesting to note that much of Merrill's success at the New York Botanic Garden depended directly on the existence of a major economic depression. In a published tribute when Merrill resigned in 1935 the Board of Managers of the New York Botanic Garden noted "in particular the promptness and foresight with which he secured for the garden the assignment of workers and appropriations of funds by various emergency relief and employment bureaus for general assistance and much-needed repairs and improvements." During the depression years the New York Botanic Garden, like many organizations of its kind, was in serious financial difficulty. Not only was the income from endowments reduced but appropriations from the city, which were the source of the labor to maintain the grounds and wages of the professional staff in the herbarium, as well as supplies such as fuel, were severely cut. In his annual report for 1933, Merrill describes the difficulties of operating the Garden on a reduced appropriation of twenty percent as compared with 1931 and the fact that capital had been expended for several years and repayments had to be made from current income.

The details of how Merrill secured assistance from public relief agencies are not known, but his annual reports while director of the New York Botanic Garden indicate the scope of financial backing (\$183,000 in 1934) which he acquired for untrained and semi-trained personnel to work in the garden and the herbarium. His reports indicate both the number of people to be supervised and the nature of the work accomplished. From the horticultural point of view it was in this period that major developments were made on the grounds of the garden. Walks were laid, roads developed, a rock garden constructed, fences built and floral displays organized and re-



organized. Appropriations from the Emergency Work Bureau and the Civil Works Administration allowed the employment of an average monthly total of eighty men in 1931, ninety in 1933 and one hundred fifty in 1934.

Women, skilled and unskilled, were available on emergency relief funds for work inside the building as mounters, artists, secretaries, librarians, clerks and technicians. In his reports Merrill speaks of seventy to ninety women employed in the herbarium and laboratories and in 1932 states the value of this assistance:

"It is impossible in this brief report to indicate in detail what this has meant to the progress of the work of the New York Botanic Garden and what it has meant to the individuals who have been given employment. It has, however, served to indicate how understaffed the New York Botanic Garden is in reference to what it is attempting to do, a fact that has long been known to the Board. The very fact that so many individuals could be employed throughout the year for productive work that has long required attention brings this situation into rather sharp relief. The employment of over three hundred individuals, with an average of over one hundred twenty per month throughout the year, has, of course, entailed distinctly heavy burdens on staff members who have had to supervise this work."

The accomplishments of this tremendous herbarium staff under Merrill's direction are indicative of the active mind of the administrator. Here was an opportunity to do herbarium work which had never existed before and which probably will never be duplicated. There was no accurate count of the total number of specimens in the herbarium of the New York Botanic Garden, so emergency labor undertook this task and a total figure was published for the first time in 1934. When the backlog of specimens in the herbarium at New York was depleted, specimens were mounted for other organizations. Merrill reports that twelve thousand specimens were mounted for the Gray Herbarium, the Arnold Arboretum and the Philadelphia Academy in 1934. Repairs were made on sheets in the New York herbarium and specimens mounted increased to 70,150 in the same year.

It was at this time, with adequate labor at the disposal of the staff, that Merrill exploited an earlier idea of placing in the herbarium proximate to the appropriate specimens, literature pertaining to those taxa. Type descriptions were copied from the literature, photostats were made and reprints cut up and the descriptions were attached either to the inside of the genus cover in the case of keys to genera and generic descriptions, or on species cover sheets for species and subspecific categories. Typists unskilled in herbarium work could prepare these descriptions and all were proofread before insertion. In the year 1934 over one hundred thousand such sheets of descriptions were added to the herbarium. In 1937 Merrill estimated that the total number of descriptions added to the herbarium at the New York Botanic Garden was "over 700,000 and it may well be greatly in excess of that number." As duplicate copies were made of all typed descriptions, the carbons were sent to other herbaria. The work continued after Merrill left New York and for many years after his arrival

at the Arnold Arboretum, he received thousands of these duplicates for insertion in the herbarium at the Arnold Arboretum.

Needless to say, the addition of seventy thousand specimens and one hundred thousand descriptions in one year crowded the standard herbarium cases and the cardboard herbarium boxes developed at California were pressed into use. Spare floor space in the herbarium was piled with these boxes as temporary housing for herbarium specimens and other boxes were piled many rows high on the top of standard cases.

In an annual report summarizing the last year Dr. Merrill was at New York, M. A. Howe reported:

"The herbarium has been growing with unabated activity. Besides the pasting in of many thousands of clippings and copies of original descriptions and cleaning and repairing specimens, 53,954 specimens have been actually added during the year. It is of note that nearly half of these additions represent Oriental specimens sent to Dr. Merrill for identification and that with the departure of Dr. Merrill, accessions from the Orient will suffer a corresponding shrinkage. Since a rate of growth similar to this has been in progress for somewhat more than five years, our herbarium cases have become full to their limit, or nearly so. We have in use at the present time more than 3,000 temporary cartons of corrugated paper in which all of our oriental material is stored. The replacement of these paper boxes alone will require about 60 standard herbarium cases and the future growth of the herbarium for the next decade may be conservatively estimated at 70 additional standard cases."

Another development possible with the surplus of labor on emergency work relief was the alphabetized series of entries for *Index Kewensis*. Merrill, years before, had seen the system of entries in *Index Kewensis* used at the Royal Botanic Garden, Kew, England, where the *Index Kewensis* is compiled and also at the herbarium in Leiden. The convenience of finding sequential entries in contrast with searching in as many as fifteen places in *Index Kewensis* was a definite advantage in herbarium work. Two teams of four women accomplished the task of cutting and pasting two copies of *Index Kewensis* in Moore loose-leaf binders. The finished books contained 2,457 pages and the labor cost was in excess of two thousand dollars.

Merrill's accomplishments at the New York Botanic Garden were great. However, he realized that the financial resources of the organization were not extensive and that the bonanza of relief labor would not last forever. He expressed this feeling in his annual report in 1932 when he stated:

"The outside plants should and must be improved preserving at the same time a definitely balanced program between scientific and horticultural work, a program however difficult to establish on the basis of our present restricted income. The New York Botanic Garden annually devotes about two-thirds of its income to maintenance and garden work, and one-third to the support of its scientific activities — just the reverse of the situation in other institutions with which we might be compared."

In 1935 Merrill received an invitation to join the staff of Harvard University as "Administrator of botanical collections." His task to ad-



minister the activities of eight and later nine separately endowed units in the field of botany. A named professorship, the Arnold Professor, was his and a recent drive had raised over one million dollars to increase the endowment. The job was indeed a challenge but this time the financial resources were greater and it appeared the task could be accomplished where a small fraction of the income need be devoted to horticulture and the large majority of funds were available for scientific work.

Merrill transferred to Harvard in the sixtieth year of his life. While he had earlier questioned in his autobiography the wisdom of changing positions at his age when he left California, he accepted the Harvard position with the understanding he would work past the normal retiring age of sixty-six until the age of seventy. Merrill actually retired at the age of seventy-two, one of only thirteen Harvard professors in the last quarter-century who were permitted to work beyond the age of seventy. Merrill therefore had ten years to accomplish the goals he outlined in his first annual report as administrator of botanical collections at Harvard. In retrospect the nature of his accomplishments speaks strongly for his abilities as an administrator and a scientist.

The position of administrator of botanical collections was created at Harvard in 1935 and Merrill was the first occupant of the post. He states "the objectives were to coordinate the work of several independently endowed units, to eliminate unnecessary duplication where possible and to integrate further the work of these units with the operations of the Department of Biology of the University." As Merrill points out:

"Professor Ames as chairman of the council of botanical collections had initiated and consummated many reforms affecting the separately endowed units. He logically abandoned the policy of isolation practiced by several of the units and adopted a new one involving closer cooperation and coordination of the work. His pioneer work established harmonious relationships between the several units in the division of biology to the advantage of biology as a whole."

Merrill's plans were to continue these interrelations with the other botanists and biologists of the university and to consolidate the physically and often intellectually separated activities. Merrill felt physical consolidation was most desirable and reports:

"It is eminently desirable that some consolidation eventually be effected but if and when this can be done depends upon a number of factors. It is a fact that Harvard University maintains three of the largest botanical libraries in America and three great herbaria. There is thus a very considerable and unavoidable duplication in purchases of both reference material, books, subscriptions to periodicals and a considerable amount of duplication of the library situation. Could some equitable plan of concentration be developed whereby the three libraries and three herbaria could be assembled in one building very material savings could be affected in maintenance charges as well as in the operation of the herbaria and the libraries. With such a change a single library would serve all three herbarium units. Such a plan would be of inestimable advantage to the three units involved not only to the elimination of duplication and even triplica-

tion but in greatly increasing the efficiency of the staff members of the now physically separated units."

Merrill's proposed solution to this was presented in his first annual report and he worked hard towards this goal throughout his years as administrator of botanical collections. His solution to problems of expansion and growth was not additions to the Administration Building of the Arnold Arboretum in Jamaica Plain and to the Gray Herbarium building in Cambridge but abandonment of these units which were to be reestablished in one central building. In 1936 he states:

"if additions be made to the two present buildings, about seven miles apart, the present unsatisfactory situation will be perpetuated. It is hoped that some practical plan of concentration can be developed thereby the herbarium and library facilities of the Gray, the Arnold and the Farlow may be concentrated in one locus."

Merrill referred to the disadvantages of the separation in all of his official reports. The strength of his feelings was emphasized in his choice of words referring to the botanical entities. "Unsatisfactory and inefficient," "can only result in stagnation and decline of productive output" "duplication or even triplication," "thoroughly unnatural, unnecessary and expensive physical separation of the library and herbarium facilities" "duplicating, triplicating and in some cases quadruplicating library purchases" are phrases often repeated in his reports.

Merrill's entreaties did not fall on deaf ears and in 1938 he apparently received an indication he should formalize his plans for a future move. With members of the Arboretum staff and through consultation with members of the organizations to be involved discussions were held and plans were drawn up. Complete blueprints of the new building were made in the summer of 1939. This building was to be located as Merrill had proposed in his reports in Cambridge between the Biological Laboratories and the Museum of Comparative Zoology and would necessitate the demolition of the Farlow Herbarium Building.

The idea, reported Merrill:

"is to bring together in one place not only the extraordinary library and herbarium facilities of the Gray, the Arnold and the Farlow but also as to the library the enormous collections of the Museum of Comparative Zoology thus forming a single comprehensive biological library. The logical place for this development is contiguous to the University Museum and the Biological Laboratory in Cambridge. This one great library would then serve all the biological needs of the University and would form a great collection of reference literature vastly superior in size and content to any similar collection of published biological data in America. . . . The ideal is one building sufficiently large to house adequately the existing reference collections of the botanical libraries and to allow for reasonable expansion. Such a consolidation would immensely increase the efficiency of all the units involved, reduce maintenance expenses, expedite the work of staff members and release for exchange or sale a vast amount of duplicate material that would no longer be needed here."



The building Merrill and his committee planned was never named although possible honors were discussed. The building was to house the collection of glass flowers on the first floor. One wing of the building was to house the combined libraries of the Arnold, Gray Herbarium, Farlow Library, Museum of Comparative Zoology and the Ames Orchid Herbarium and Library on five full floors and three additional half floors and these would occupy over 24,750 square feet of floor space. The major portions of three floors would be utilized as herbarium space. Only two offices were planned in the building for the staff was to occupy tables in the herbarium following the systems then in use at both the Gray and the Arnold. The facade of this very modern building would bear the names of Arnold, Gray and Farlow and the building could be built and equipped for less than one million dollars. In the fall of 1939 the international situation worsened with the outbreak of war in Europe and the concomitant restrictions imposed in the United States. It was soon apparent that construction of a major building at that time was impossible and unpatriotic. Thus the well drawn plans for consolidation of botanical resources at Harvard were laid aside for the duration of the war.

Merrill began his career at Harvard with an office in the Gray Herbarium building in Cambridge. His personal concern however was the administration of the funds of the Arnold Arboretum and only the supervision and coordination of activities of the eight other privately endowed institutions. After the first year he transferred his headquarters to Jamaica Plain when the University acquired a residence for the director of the Arnold Arboretum which appended the grounds. Merrill lived in this house on 960 Centre Street until the time of his death. This residence became a mecca for visiting botanists who at the same time could be within one hundred yards of the Administration Building with its fine herbarium and the famous collection of trees and shrubs on the grounds.

To assume responsibility for horticulture and the care of the grounds Dr. Merrill added for the first time the position of "Horticulturist" to the staff of the Arboretum, and the horticulturist, assisted by the propagator and superintendent of buildings and grounds, assumed the responsibility for the living collections allowing Merrill to devote his undivided attention to the herbarium and library and his personal research on Asia. The interest of the Arboretum in the flora of Asia dated from the period of Sargent and reflected especially the field activities of E. H. Wilson. Wilson was a botanical collector with an eye of appreciation for the potential ornamental trees and shrubs of the area. Wilson collected herbarium specimens for vouchers of the seeds and for more detailed study of the plants considered useful as ornamentals. Wilson had died before Merrill's appointment at Harvard and in his first year, with sufficient funds for such activities Merrill began a program of field work, supporting native botanists in their home area with small grants of money to enable them to collect specimens and to send seeds of the most promising ornamental plants seen. The initial grants went to Chinese botanists but eventually support was extended to botanists in Japan, Korea, the Philippines and in fact most areas of

Asia where botanists existed. During two years of Merrill's administration as many as fourteen botanists and institutions were conducting field work subsidized by the Arnold Arboretum. The number dropped during the war years and increased immediately afterward. It wasn't long before the specimens began to arrive at the Arnold Arboretum. Some were identified, but the majority were not. In this situation Merrill was at his best. Few botanists could match Dr. Merrill in "spot" identification of material from Asia and it was a rare plant which was not immediately analyzed with a selective eye and placed in the proper genus and family or if too common promptly discarded. Those selected for further study went promptly to the mounters and the number of specimens prepared for insertion in the herbarium increased. Space to house these specimens soon became critical for the new additions soon outgrew the space available in the standard herbarium cases. Once again Merrill resorted to the cardboard herbarium cases developed at California and used again at New York to meet the same situation of rapid expansion. Display rooms for museum collections open to the public soon were pre-empted for herbarium storage and every nook and cranny began to hold cardboard herbarium boxes of specimens.

In the herbarium proper Merrill introduced the ideas he had developed earlier at New York and California. Ten phytogeographic areas were designated with a different colored folder for each area. The organization of this system in a herbarium of half a million specimens was a major undertaking for the botanists on the staff.

The Arboretum possessed copies of *Index Kewensis* and here again Merrill carried out the alphabetization of entries which had been done at New York with emergency labor funds and relief workers. The principal difference was that at the Arboretum the work was done by the professional botanists on the staff.

The system of clippings begun at New York was also continued by Merrill on his arrival at Harvard. Perhaps foresightedly Merrill had had carbon copies prepared and while some of these were sent out gratis from New York Merrill formalized the agreement while at Harvard and helped support a continuation of this work at New York with the originals coming to the Arnold Arboretum. While it is true these clippings save an enormous amount of work and decrease the necessity of going to the library for original descriptions their method of insertion began to add to the bulk in an already overcrowded herbarium. The species covers with the attached descriptions were often thick. In many cases both genus and species covers were prepared for descriptions where there were no specimens. In other cases several sheets of paper were involved for species reduced to synonymy and so descriptions were filed in two or more places in the herbarium. Various measures were taken to relieve temporarily the congestion present in both the herbarium and the library. More American material was transferred on semi-permanent loan to the Gray Herbarium, thereby increasing their problems of handling and storing the specimens. The orchids were transferred to the Ames Herbarium in the botanical museum. A large col-



lection of books dealing with forestry were transferred to the Harvard Forest in Petersham, Massachusetts. Some of the older pre-linnean works were transferred for more satisfactory protection to the rare book library of Harvard. Within the herbarium proper there was absolutely no room for insertion in sequence of newly mounted materials and so a second family sequence was started on the tops of the steel cases by storing mounted sheets in cardboard cartons. Tables and alcoves formerly used by staff and visitors were confiscated for specimens. Display materials were stored in the barn and the collection of wood specimens and slides were moved to space in the biological laboratories in Cambridge.

Each innovation while improving the usefulness of the herbarium proved expensive, in the cost of professional staff time for the work, in the materials and in compounding the already crowded situation in the herbarium.

In the meantime at Harvard Merrill's research on the floras of Asia increased. Horticultural work caring for the grounds and meeting the public was adequately handled by the new horticulturist. Identifications of horticultural plants were the interest of Alfred Rehder. Funds for the first time in Merrill's career were adequate for taxonomic research and purchase of specimens or support of foreign collectors and as the new collections were studied his personal production of scientific articles jumped.

Using the extensive library resources of the Arboretum he published alone and with co-authors a "Polynesian Botanical Bibliography" of 194 pages and a "Bibliography of Eastern Asiatic Botany" of 719 pages. He maintained and increased his bibliographies of the Philippines and for other island areas which unfortunately were never published.

His interest in validating botanical names led him to study critically the descriptions of older and often ignored botanical publications. The work of Otto Kuntze on plants from Indo-china, Palisot de Beauvois. Houttuyn, Muhlenberg and Rafinesque on plants from America revealed many combinations unrecorded in *Index Kewensis* which affected the nomenclature of plants from America as well as Asia. Feeling strongly that these works should be consulted more frequently but recognizing that the volumes were rare and unavailable Merrill instituted a technique to reproduce many of these rare volumes by lithoprint. The copies in the library of the Arnold Arboretum were used in the process but the work was financed largely through private funds supplied by Dr. Merrill.

The specimens in the Linnaean herbarium were also considered by Dr. Merrill to be too inaccessible to most American botanists and he encouraged the recording of these specimens and their available data on microfilm. This was accomplished during the war years through a grant from the Carnegie Foundation. When the Arnold Arboretum received these microfilms Dr. Merrill had 5×7 glossy prints made of each and mounted on stiff cards approximately twice that size. The complete data from Savage's catalogue was printed with the photograph and together these data form a valuable research tool.

His taxonomic interest turned to New Guinea with the prospect of an expedition visiting that area and in 1936-1937 the Arnold Arboretum sup-

ported financially the botanical efforts of the second Archbold Expedition to that immense island. All of the specimens collected by the botanists were sent to the Arboretum where the collections were studied, labels prepared and the duplicates distributed. The same arrangements were made with successive expeditions to the area and in these plant collections came close to a thousand plants new to science. As co-author with Dr. Lily Perry of the Arboretum staff there began in the *Journal of the Arnold Arboretum* the series, "*Plantae Papuanae Archboldianae*" of which Number 18 was published in 1949.

Merrill's familiarity with the Pacific Islands and the vegetation of that area proved of great value during the war years. He was frequently called to Washington for consultation and the full record of his service will probably never be revealed. In 1945 he was the recipient of the Appreciation Certificate for his services as Consultant to the Secretary of War. With the assistance of Mr. Gordon Dillon on the art work, Dr. Merrill compiled a handbook of the "Emergency food plants and Poisonous plants of the islands of the Pacific" which was published by the government as a War Department technical publication. The illustrations and the text of this booklet were reproduced in many of the survival manuals issued by the branches of the military service. In this publication Dr. Merrill's personal experience as well as the excellent library and herbarium resources of the Arnold Arboretum were evident. This book remains extremely useful to the botanist for the compilation of local and dialect names for the common plants of the Pacific Islands. As part of the education program for our troops in the Pacific theatre several books on wild life and natural history were published. Dr. Merrill contributed the material on plants in "*The Pacific World*" which was edited by Fairfield Osburn and later wrote the more comprehensive "*Plant Life of the Pacific World*" which was published with hard covers by the Macmillan Company and in a pocket and paper cover edition by the Infantry Journal as one of the Fighting Forces editions. In these booklets Dr. Merrill described the technique for collecting plants as scientific records of the vegetation of the area. In response to many inquiries Dr. Merrill was always encouraging, and correspondents wherever they might be stationed were invited to send plant specimens in for determination. With the assistance of other members of the Arboretum staff these plants were identified, some interesting facts about the collection or the taxon related and the determination promptly returned. Many commanding officers and postal censors considered such activities as violation of security regulations and many shipments of specimens were confiscated and sent to government agencies or destroyed.

When the war in Europe ended and it appeared only a matter of time before hostilities in the Pacific would be over Dr. Merrill renewed his requests for a consideration of the problems of the herbaria and libraries he supervised. The continued increase in the Harvard University herbaria during the war years had completely filled all available space and the libraries were overflowing the shelf space available. Dr. Merrill suggested that the plans for a consolidation and the construction of a new building



which had been drawn up and tentatively approved in 1938 and 1939 should be reviewed for quick action once the war was over and building restrictions lifted. In 1944 Dr. Merrill was sixty-eight years old, three years beyond the normal age at which professors are normally freed of administrative duties and two years beyond the normal retirement age. In view of Dr. Merrill's expected retirement at age seventy, the Provost asked Professor I. W. Bailey, professor of wood anatomy on the staff of the Arnold Arboretum and senior botanist in length of service to Harvard, to review the previously drawn plans and submit a confidential report. This report entitled "Botany and its applications at Harvard" was written with the consultation and advice of the botanists in the many botanical institutions at Harvard and was approved by them all. Dr. Merrill moved for the acceptance of this report at the faculty meeting where it was submitted and Dr. Fernald, then director of the Gray Herbarium, seconded the motion. The report was approved on March 1, 1946, by the President and Fellows in their joint role as Administrators of Harvard College and Trustees of the Arnold Arboretum. The program proposed repeated Merrill's call for the erection of a single building to house the herbarium and library collections of the several botanical institutions at Harvard, as well as some administrative changes. The new building was to be in the location proposed earlier by Dr. Merrill but would not be as all-inclusive as he had originally visualized, for it did not seem practical to house the libraries of the Biological Laboratories and the Museum of Comparative Zoology in one unit. However the combination of libraries and herbaria proposed would reduce the duplication of purchases and expenditures, provide new and larger quarters and allow room for expansion and bring staff members of similar interests in closer association for mutual benefit.

Construction of the new herbarium building was delayed until wartime restrictions on building were lifted and in the meantime further discussion of the proposed administrative reorganization took place. The new building was finally erected in 1953 and occupied in 1954, eighteen years after it was first proposed by Dr. Merrill.

When Dr. Merrill was no longer involved in the affairs of administration of the Arnold Arboretum he directed his attention full time to his research. The contacts which he once had had with botanists in Asia were reestablished and supported by grants from the Arboretum and these men again began to send collections for Dr. Merrill's attention. Special mention should be made of the efforts of Dr. Merrill to supply his botanical friends with the necessities as well as a few of the luxuries of life in their post-war existence under rationing restrictions. To Asia and to Europe Dr. Merrill directed packages he himself prepared. His contributions in the form of CARE packages will never be forgotten as an indication of his extreme concern and generosity for his friends.

One botanical expedition in China collecting for the Arnold Arboretum located fruiting trees of *Metasequoia* which Merrill described as another "living fossil." This exciting discovery opened a new vista and Dr. Merrill became a modern "Johnny Appleseed," for he acquired several bushels of

these seeds which he distributed widely for trial. At one European horticultural meeting Merrill made a lasting impression by appearing on the speakers' platform his pockets bulging with what proved to be the seeds of this most unusual plant. His interest in the distribution and the success of this introduction lasted until his death.

Dr. Merrill had been on the selection board of the Guggenheim Foundation for many years and contributed valuable service in the screening of the many applications. In 1951 he in turn was the recipient of a grant, the first of several grants from the Foundation which enabled him to spend six months in Europe where he visited many of the major herbaria. He examined many of the types of Asiatic plants, making critical notes and carbon paper tracings. At the British Museum he worked over and identified many old collections and selected for the Arboretum a number of available duplicates of the Carr collection from New Guinea. At Brussels he critically studied the Roxburgh specimens in the Martius herbarium and prepared a list of the plants and their identifications. Carbon copies of this list were sent to the several institutions maintaining an interest in such Asiatic collections, but unfortunately the data have not been published. It was unfortunate that Dr. Merrill suffered another severe heart attack while on this European trip and from that time on was advised to limit his activities and restrict his travel. It meant that he had to give up his winter trips to Cuba, Honduras and Panama and he found the New England winters more difficult to endure. His thoughts remained in the tropics, however, and he reacted violently to some well-publicized theories of transpacific migration of plant materials involving raft travel and human agencies. The problems of distribution of American crop and weed plants in the Pacific and Asiatic plants in the western hemisphere had long been of interest and concern to him. As early as 1904 he had published on "The American element in the Philippine Flora" and at the end of the war he investigated the species introduced in the region of Manila by military activities. His last few years were spent in examining the manuscript records of the early expeditions to the Pacific islands. His observations and opinions were expressed in typical Merrillian fashion in his final publication, "The botany of Cook's voyages and its unexpected significance in relation to anthropology, biogeography and history," published by *Chronica Botanica* in 1954.

Merrill is survived by his widow, Augusta Sperry Merrill and one son, Dudley. His ashes are to be interred in a family plot in East Upton, Massachusetts.

In retrospect only one word can satisfactorily describe Elmer Drew Merrill and his contributions to the knowledge of botany. He was a builder. His handiwork is evident in many parts of the world. In herbaria alone Merrill must receive credit for amassing outstanding collections. The two thousand specimens collected as a student at the University of Maine were given to the New England Botanical Club. In the Philippines he began the herbarium of the Bureau of Science which in 1922, two years before his departure, contained two hundred seventy-five thousand mounted



sheets. At California, herbarium accessions in the two years before Merrill's arrival averaged 8,250 sheets but swelled from 27,000 to 37,000 sheets a year during and immediately after his administration. His own estimate of the increase in the herbarium at the University of California during his stay there was 110,000 sheets. During the short period of his directorship of the California Botanic Garden an herbarium was started and built up to over 180,000 sheets. From 1930 to 1935 Dr. Merrill, as director of the New York Botanical Garden, increased the herbarium under his supervision by over 280,000 mounted specimens and to this must be added the insertion of over 700,000 sheets of descriptions of plants. At Harvard, too, the herbaria felt his influence, for the herbarium of the Arnold Arboretum, founded in 1872, increased over fifty percent in size during the term of his directorship, from 409,000 to 631,000, while at the same time, in excess of 130,000 sheets were transferred to the Gray Herbarium, the Farlow and Ames Herbaria. Thus, one man has accounted for the amassing of botanical resources totalling over one million sheets of herbarium specimens and untold numbers of duplicates distributed for the benefit of the botanists to follow him.

Our path has been made clearer by his keen mind and his extensive record of publications. Nearly five hundred titles are credited to his pen, for he published one hundred forty-five significant papers and books on the flora of the Philippines, fifty-four on China, thirty on New Guinea and more than a dozen each on islands such as Sumatra, Borneo and Java. His desire for simplification in the citation of technical journals led to the adoption of one-word titles for periodicals such as *Brittonia* and *Sargentia*, which he helped create, or *Hildgaardia* and *Arnoldia*, which replaced more cumbersome names. While he had few students to carry on his work, his influence of position and personality carried respect and won for him many times the honor of having his name associated with a living plant. The genera and species named by him number more than a thousand and those named for him are more than a dozen. *Magnolia* "Merrill" carries his name in the north, as does the Merrill Palm (*Adonidia merrilli*) in the tropics.

It can be said with respect and appreciation that he made his immortality through the plants that he loved.

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## A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS \*

GRADY L. WEBSTER

*With twelve plates*

### LEAF

#### Lamina.

The leaf-blade in *Phyllanthus* (and in the other genera of Phyllanthaceae as well) is invariably simple and entire, but there are many variations of size, shape, and texture. In a few species such as *P. urinaria* and *P. carnosulus* there may appear to be a minutely serrate or crenate margin, but this appearance actually is due to projections of individual or associated epidermal cells which belong in the category of trichomes; true vascularized teeth never occur.

The leaf of *Phyllanthus* varies in size from minute, as in *P. imbricatus* where it may be only 1.5 mm. long, to large as in *P. grandifolius* where it may attain 15 cm. in length and almost as much in width. It is not surprising that the leaves of *P. grandifolius*, which are borne on permanent branches, are large and persistent; but a few species, such as *P. juglandifolius* and *P. cornifolius* with the foliage leaves only on deciduous branchlets also have leaves 15 cm. long, although never as broad. On the whole, the leaves of *Phyllanthus* are medium-sized or small, and the median for the genus would perhaps fall at about 3 cm.

Most species of *Phyllanthus* have elliptic to oblong leaves, but as might be expected in so large a genus, there are some striking deviations. In some New Caledonian and South American species (e.g., *P. bupleuroides* and *P. duidae*) the lamina is prominently basally lobed and has the outline of a *Cercis* leaf-blade. A few xerophytic species such as *P. comosus* and *P. formosus* (sect. *Orbicularia*) have leaves with a pronounced spatulate outline. The apex of the blade varies from retuse to acuminate among various species, and in some of the Cuban species of sect. *Orbicularia* there is a long attenuate scarious tip, which however is differentiated from the rest of the leaf-blade. A pronounced "drip-tip" such as characterizes the leaves of many Lauraceae in the tropical rain forest is scarcely developed in any species of *Phyllanthus*.

Leaf texture within the genus runs the gamut from extremely tenuous and delicate as in *P. tenuifolius* (sect. *Cyclanthera*) to rigidly coriaceous in species of several sections (e.g., *Orbicularia*). The leaf surface is usually smooth, although many species have a papillate lower epidermis. *Phyllanthus acuminatus* is exceptional in having definitely scabrid leaf-surfaces.

\* Continued from volume XXXVII, page 122.

Rothdauscher (1896: 8) regarded the monotony of anatomical features of the leaf as virtually a tribal character of the *Phyllanthae*. However, while it is doubtless true that a greater diversity exists in other tribes such as the *Crotoneae*, the various histological characters within *Phyllanthus* provide data of considerable classificatory and evolutionary interest. Froembling (1896) indeed concurred with Rothdauscher in remarking on the great uniformity of leaf structure in the subtribe "*Euphyllanthae*". But although he studied over sixty species of *Phyllanthus* (s. str.) he did not investigate a single species of sects. *Elutanthos*, *Williamia*, *Orbicularia*, or *Epistylum*, which together make up the great majority of the woody West Indian species. It is not surprising, therefore, that his observations require some modifications on the basis of various features of the species in those groups. In the following account the remarks apply particularly to the West Indian species, although they often are relevant for the entire genus as well.

In the woody species of *Phyllanthus* the upper epidermis, overlaid by a cuticle which may attain considerable thickness, is made up of more or less vertically elongated cells with outer tangential walls that are polygonal in outline. The cells of the lower epidermis are usually much smaller in surface area, inclined to be more undulate in outline (or at least less sharply polygonal), and are tangentially elongated. In the herbaceous species with thin leaves, however, the cells of the upper epidermis are not sharply polygonal in outline, and in some species the perimeter of both upper and lower epidermal cells is undulate.

Froembling (1896: 69) was content to characterize the stomata of *Phyllanthus* as extremely variable with regard to the number of subsidiary cells. However, in the leaves of the woody species the stomata are clearly the "rubiaceous" type as defined by Metcalfe and Chalk (1950: xv); there are either two — or apparently by one redivision — three subsidiary cells with their long axes parallel to the opening between the guard cells (PLATE-FIG. 18). But in leaves of herbaceous species this arrangement may become obscured due to the more irregular cell outlines. Often the guard cells are surrounded by three subsidiary cells, two parallel to the long axis of the stoma and one more or less perpendicular; such a stoma might be considered to belong to the "cruciferous" type (PLATE-FIGS. 19 & 20). In some herbaceous species such as *P. polygonoides* the arrangement is still more obscure because here there may be a number of subsidiary cells which scarcely differ in outline from the rest of the epidermal cells, and in this case the stoma would have to be classified as "ranunculaceous". Or, in the case of a number of species such as *P. niruri* there may be more than one type on the same leaf (PLATE-FIG. 21). The herbaceous species often show a significant difference in distribution of the stomata, as they often have them on both surfaces of the leaf, whereas in the woody species they are always confined to the lower epidermis. Taking the genus as a whole, there is no doubt that the basic stomatal type is the "rubiaceous", which Rothdauscher observed to be the prevailing type in the other genera of *Phyllanthae*.



The mesophyll in those species of *Phyllanthus* investigated thus far is composed of typical palisade and spongy parenchyma of "bifacial" leaves. The three species of "*Phyllanthus*" in which a foliar hypoderm was reported by Froembling (1896: 69) prove to belong to other genera. Among the West Indian species of *Phyllanthus* a definite hypoderm has been observed only in *P. myriophyllus*, although it perhaps may be discovered in other species. The palisade tissue is usually made up of a single layer of very slender cells; in coriaceous leaves with a large volume it is the spongy rather than the palisade parenchyma which is increased in bulk. Froembling reported unusual palisade cells only in the species of the Old World section *Eriococcus*. In *P. elegans* (the only species of the section which has been introduced in the West Indies) Froembling found that the portion of the cell bordering the epidermis is enlarged so that the entire cell has a clavate shape; and in *P. roxburghii* this enlarged portion is lobed so as to have the outline of a mitten. No such unusual palisade cells have been detected in any of the native West Indian species. The spongy mesophyll in the leaf of *Phyllanthus* is composed of parenchyma cells which may be arranged compactly to loosely; in some of the species of sect. *Hemiphyllanthus* the spongy layer has a striking areolate appearance due to the regular organization of the cells around circular lacunae.

Froembling reported that the veins in the *Phyllanthus* leaf are all of the embedded type, as opposed to the veins of other Phyllanthaceae which Rothdauscher designated as "durchgehende"; in the latter the sclerenchyma or collenchyma associated with a vein is expanded into wings which abut on the upper and lower epidermis ("vertically transcurrent" veins of Metcalfe and Chalk, 1950; xvi). During the present study of the West Indian species of *Phyllanthus*, however, both types were observed. In *P. discolor* (sect. *Williamia*) there are vertically transcurrent veins with bundle sheath extensions (Esau, 1953: 430) of collenchyma cells interrupting the palisade layer and reaching both epidermises. But within the single sect. *Orbicularia* both types have been observed. *Phyllanthus orbicularis* has rigidly coriaceous leaves with conspicuous sclerenchymatous bundle sheath extensions which tend to become uniseriate above and multiseriate beneath, as in *P. discolor*. But in the related *P. scopulorum*, which has flexibly coriaceous leaves, the veins—though armed with sclerenchyma—are clearly embedded (PLATE-FIG. 22). Some of the species with coriaceous leaves in other West Indian sections (e.g., *Thamnocharis*) resemble *P. scopulorum* in having embedded veins with massive sclerenchymatous but extensionless sheaths. In these species the rigidity of the leaf-blade is enhanced by the very massive bundle of fibers which is associated with the marginal vein and which is responsible for the prominent rim-like margin of the leaf (PLATE-FIG. 23).

The veins of the *Phyllanthus* leaf are pinnately branched, and the laterals ordinarily ramify considerably and then unite near the margin to produce an arcuate marginal vein. The foliar vascular systems of individual species differ widely from one another in such details as branching pattern, massiveness, development of parenchyma vs. sclerenchyma in

bundle sheaths, and vein endings; consequently, despite the great variation in some of these characters, leaf vascular tissue appears to be a promising source of systematically valuable criteria. In species with membranous or chartaceous leaves, only the midrib and larger veins are jacketed with sclerenchyma; and the ultimate veinlet tips lying free in the mesophyll are bordered (if at all) only by parenchyma sheath cells. The veins of many species end with one or two essentially unmodified tracheids (PLATE-FIGS. 28, 30); but in other species one or more of the terminal tracheids are modified into swollen "storage tracheids" ("Speichertracheiden"; PLATE-FIG. 29). In some species with coriaceous leaves, however, the fibers of the bundle sheath extend out even to the ends of the minor veins; and in several species, such as *P. microdictyus*, the sclerenchymatous elements flare beyond the tips of the last tracheid (PLATE-FIG. 24).

The designation of these sclerenchymatous elements presents a rather difficult problem in terminology. In the following discussion these elements which project into the mesophyllar spaces of the leaf will be called "foliar sclereids", following the usage of Foster (1946). The sclereids of *Phyllanthus* would mostly belong to either Type III or Type IV of Foster's classification, for they are always elongated and not highly branched. In fact, except for their position and occasional branching the sclereids of *Phyllanthus* could just as well be called fibers. However, in a few species (e.g., *P. chryseus* and *P. comptus*) the sclerification of the veinlet-ends is due to peculiar, sometimes deformed, sclerenchymatous elements which are more or less intermediate between sclereids and tracheids (PLATE-FIG. 31).

Within the evolutionary series formed by the three related sections *Williamia*, *Williamiandra*, and *Orbicularia*, a trend of increasing sclerification is strikingly apparent. In the most primitive species of the complex, *P. discolor*, the ultimate veinlets are naked. The other species of sect. *Williamia*, *P. microdictyus*, exhibits sclereids which project beyond the veinlet-tips, as mentioned above. In sects. *Williamiandra* and *Orbicularia* the exertion of the sclereids has become far more pronounced, and the massive veins and free-lying portions of the sclereids occupy a very appreciable portion of the volume of the leaf (PLATE-FIGS. 25-27). In sect. *Williamiandra* (and sometimes in *Orbicularia*) many of these elongated sclereids extend vertically through the leaf as columns which abut against the upper and lower epidermis in the manner of the Type III sclereids illustrated by Foster for *Mouriri pusa* (1946: fig. 16). It is furthermore very interesting that sclereids of this kind have arisen independently in *P. duidae*, a species of the unrelated South American sect. *Microglochidion*.

On the basis of the observations made so far it can be said that the foliar sclereids of *Phyllanthus* appear to be terminal in origin and to have been derived from the fiber-like sclerenchymatous cells of the bundle sheath. Diffuse sclereids or stone cells have not been observed in the leaf of any species of *Phyllanthus*. Furthermore, foliar sclereids have thus far been detected only in the New World species. However, since they have originated independently in the West Indian and South American species,



there is no reason why they could not occur in some of the Old World species; further investigation of the leaves of the latter is therefore desirable.

As Froembling reported, almost all species of *Phyllanthus* which have been examined prove to have crystals, most often druses, in the mesophyll. In a smaller but still considerable number of species rhombic or prismatic crystals are produced as well. There is a definite tendency for the druses to occur in the layers of cells directly adjacent to the upper and lower epidermis, but occasional ones may also be found scattered in the mesophyll, and both druses and rhombic crystals may occur along the veins. The use of crystals as a taxonomic character is attended with the disadvantage that their expression may vary within a single species and that they may change form in cleared mounts which have been treated with caustic soda, as reported by Heintzelman and Howard (1948). It appears doubtful that the study of crystals will afford much assistance in distinguishing closely related species; but it is possible that a sufficiently broad survey might provide useful evidence on the supraspecific level. For example, the species of sect. *Orbicularia* appear to differ from most of the related sections such as *Williamia*, *Epistylum*, and *Thamnocharis* in having both rhombic crystals and druses, while the latter have druses alone.

### Petiole.

The petiole of all species of *Phyllanthus* is quite short and never approaches the length of the blade. Ordinarily it has an uncomplicated form, being plane adaxially and more or less convex abaxially, sometimes with a flange of green tissue decurrent from the blade. In sect. *Asterandra* this flange is very distinctively modified by transverse pleating into an accordion-like shape, so that isolated leaves of this group are always easy to identify.

Anatomically, the structure of the petiole conforms to the simplicity of the external form. The epidermis consists of small squarish cells, and stomata have not been observed. The vascular tissue as seen in cross-section (PLATE-FIG. 5) assumes the form of a slightly adaxially concave arc, with no conspicuous wings, flanges, or exclaves of vascular tissue such as have been reported in the petioles of many Euphorbiaceae (Dehay, 1935). In *P. urinaria*, however, the usual situation is modified by the presence of a curious reticulum of many fine inter-connected tracheids which form a mesh on all sides of the central vascular core. This accessory tracheary tissue is probably correlated with the pulvinate nature of the petiole; the leaves of *P. urinaria* have been reported to be "sensitive" to touch.

Crystals are usually more abundant in the petiole than in the blade, and the proportion of druses to rhombic crystals may be different. Sclerenchyma often forms a conspicuous jacket around the vascular tissue, but no free sclereids or stone cells have been observed.

### Stipules.

The leaves of *Phyllanthus* are always stipulate, although in some species the stipules are evanescent and thus at first sight may appear to be absent. Most commonly the stipules are triangular to lanceolate with an acute or acuminate, sometimes reflexed, tip. The margins and tip are usually scarious at maturity and are differently colored from the herbaceous basal area. The scarious portion of the stipule is composed of tabular cells without stomata and is often denticulate at the margin. The basal herbaceous portion, which may have stomata, is often thickened and persistent after the fall of the scarious tip.

Although the stipules of *Phyllanthus* never become as large and foliaceous as in species of *Amanoa* or *Drypetes*, they do show extensive variations in duration, size, shape, color, development of auricles, marginal toothings, etc. For this reason they provide some of the most convenient characters for readily distinguishing species. Measuring the sizes of stipules has the slight inconvenience that those of the proximal portion of branch or branchlet are usually larger than the distal ones; and the two at the same axil may be unequal. In *P. formosus* the two members of each stipule-pair are extraordinarily unlike, one of them being broad and conspicuously lacerate-dentate while the other is narrow and quite entire. This approaches the extreme heteromorphy of the stipules in *Vicia monantha* as illustrated by Glück (1919: fig. 2).

The species other than *P. formosus* do not have such a dimorphism of stipules on the same branchlet. However, in most species with phyllanthoid branching the stipules on the deciduous branchlet are quite different from those on the permanent axis; the latter are usually larger, broader, and of a much firmer texture. In many woody species these permanent-branch stipules are clustered at the apex of the stem into a dense scaly cone which encloses the apical meristem and unexpanded leafy branchlets. In such woody species as *P. cinctus* these stipules are indurate and the numerous parallel veins are stoutly armed with sclereids. In most herbaceous and some woody species of *Phyllanthus* the stipules have only a single vein which is not jacketed with sclereids (PLATE-FIG. 5).

### Cataphylls.

In the section on growth form one of the essential characters of phyllanthoid branching was shown to be the reduction of the leaves on the seedling stem (and all subsequent persistent axes) to cataphylls, the reduced leaf blade usually resembling the stipules in appearance and thus three stipules appearing to be at the same axil. Actually, although the reduced blade of the cataphyll is usually just like the stipules in texture and color, it is very often narrower and thus may be distinguished by its shape and position.

The spatial relationship of the cataphylls in *Phyllanthus* is rather peculiar. They do not correspond to conventional cataphylls as defined, for instance, by Gray (1879: 401) or Goebel (1905: 384). As Goebel pointed



out, the term was originally coined by Schimper to refer to the scale leaves on rhizomes or the basal parts of aerial stems. Goebel added:

"To these leaf formations, both in their construction and function, all those epigeous parts which have been called bud scales (tegmenta) conform, and so closely that they have received the same name. This is not altogether wrong, inasmuch as these leaf formations upon an upright growing shoot stand upon the "lower" region of the shoot and are followed by foliage leaves."

The cataphylls of *Phyllanthus*, however, do not correspond either to rhizome scales or bud scales, for they definitely appear on the upper portions of stems and branches and are *preceded* by typical leaves. Their position on the axis therefore appears to be the reverse of that of typical cataphylls. Jackson (1905: 131), would have called the scale-leaf of *Phyllanthus* a "hypsophyll", which is defined by him as "a bract of the inflorescence, a reduced or modified leaf towards the upper end of the shoot." As Goebel (1905: 390-391) remarked, however, it appears best to retain the word "hypsophyll" for those leaves directly associated with flowers. In form and evidently in function the scale-leaves of *Phyllanthus* resemble typical cataphylls, and their different position does not appear to be of fundamental importance. The main difference between the cataphylls of *Phyllanthus* and most bud-scales is that the latter are associated with seasonal growth.

Majumdar and Arshad Ali (1956) have studied the vascular anatomy of the cataphylls in *Phyllanthus amarus* ("niruri") and *P. reticulatus*. They report that in *P. reticulatus* (which has trilacunar nodes) the traces from the lateral leaf-gaps of the node run into the stipules; the median trace gives off two branches which turn back and join the stipular traces. This observation has been personally verified as far as the branchlet of *P. reticulatus* is concerned. In *P. amarus*, on the other hand, they report that the main axis has unilacunar nodes (although the nodes of the deciduous branchlet are trilacunar) and that the two lateral branches of the median trace (midrib) pass directly into the stipules. Because of this difference they call the appendages of the *P. amarus* cataphyll "leaf lobes" and those of *P. reticulatus* "stipules"; but then they qualify this by adding that the difference between basal lobes and stipules in this case "is one of degree [rather] than of kind". It is difficult as yet to evaluate these very interesting observations on the basis of the nodal anatomy of only two species of a genus as large as *Phyllanthus*. Despite the behavior of the traces, there is no difference in the cataphyllar stipules of *P. amarus* and *P. reticulatus* which would warrant giving them different names. Furthermore, the fact that the leaf-blade of *Phyllanthus* is always simple and entire quite precludes the possibility of *P. amarus* having three-lobed leaves. What the researches of Majumdar and Arshad Ali do show is that, as might be expected, the foliar traces of the advanced herbaceous species *P. amarus* have undergone considerable modification and reduction as compared to the more primitive *P. reticulatus*.

Anatomically the blade of the cataphyll in *Phyllanthus* is completely

different from the foliage leaf and closely resembles the accompanying two stipules. Stomata, palisade cells, and spongy parenchyma are lacking (at least in the expanded scarious portion), the epidermal cells are tabular and thick-walled, and the veins (if more than one) are parallel. In some of the herbaceous species of sect. *Phyllanthus* transitional forms between foliage leaf and cataphyll occur, particularly at the proximal nodes of permanent branches. These have a green foliose proximal part which distally is abruptly contracted into a brownish scarious tip. The cataphyll of some of the species of sect. *Orbicularia* (e.g., *P. scopulorum*) is especially interesting because the blade closely resembles the long scarious deciduous tip of the foliage leaf. This suggests that in some species of *Phyllanthus*, at least, the cataphylls would belong to the category of those derived mainly from leaf apex (cf. Schulze, 1934). However, drawing a strict homology between leaf apex and cataphyll blade would scarcely be justified until comparative developmental studies have been made.

Dingler (1885: 139) found in studying the seedling of *P. niruri* that the reduction of the foliage leaf to cataphyll occurs at the node where the first deciduous branchlet is attached; he therefore concluded that there is a direct causal relationship at work. It might be supposed, consequently, that it is the precocious expansion of the branchlet which inhibits the lamina of the cataphyll. However, the correlation between reduction of cataphyll blade and development of deciduous branchlet does not appear to be as exact as Dingler suggested. Examination of seedlings of *P. abnormis*, *P. amarus*, and *P. tenellus* has shown that the abrupt change from foliage leaf to cataphyll by no means takes place at precisely the same node where the first deciduous branchlet appears. Furthermore, there are a number of species (e.g., *P. formosus*, *P. berterianus*, and *P. sellowianus*) with undoubted phyllanthoid branching in which the reduction of foliage leaf to cataphyll takes place considerably later in ontogeny or not at all. Nevertheless, there is in a general way an undoubted inverse correlation between development of deciduous branchlets and the blades of the leaves on the permanent axes.

### Trichomes.

The great majority of the species of *Phyllanthus* may be described as completely glabrous, but many of them have a papillate lower epidermis, and in a few species papillae may occur on the upper leaf-surface as well. As Froembling pointed out, there are some species (e.g., *P. praetervisus*) in which all manner of transitions may be observed between epidermal cells which have merely a convex outer wall to those in which the cell is drawn out into a long hair. The hairs are uniseriate, composed of one to several cells, thin-walled, and usually obtuse at the ends. Foliar glands or capitate hairs of the sort found in the Crotonaceae are unknown in the Phyllanthinae. Froembling's report that unicellular hairs of *Phyllanthus* often assume a nearly uncinatiform form probably applies to species now included in *Glochidion*; in both genera, however, the hairs are never as long, sharp-pointed, and pronouncedly uncinatiform as those in the Andrachninae.



Among the native West Indies species well-developed trichomes occur in only a few groups. In sect. *Elutanthos* multicellular hairs occur on both stem and leaf, but their expression is quite variable, and *P. botryanthus* is completely glabrous. In sect. *Hemiphyllanthus* trichomes occur only on the axes, where they are clustered on peculiar longitudinal plates or ridges of cells. The result is an incrustate appearance which recalls that of the twigs in sect. *Williamiandra*, which have incrustate masses of cells that are derived from proliferation of lenticellar tissue.

### INFLORESCENCE

The best general treatment of the inflorescence of the Euphorbiaceae (excluding the Euphorbiae!), despite its age, is that of Baillon (1858). He clearly stated that the cymose pattern is the most widespread and fundamental both in the Euphorbiaceae and the angiosperms as a whole. The study of the inflorescence of *Phyllanthus* agrees well with this and with the hypothesis of Rickett (1944) that the *dichasium*, or "complete cyme" of Gray (1879) is the basic type of which all other angiospermous inflorescences represent modifications. In many Euphorbiaceae the flower arrangement has become so highly modified that its fundamentally cymose nature is apparent only on careful inspection. In *Phyllanthus*, however, there is little doubt except for those few species with solitary flowers; and there is furthermore a broad spectrum of inflorescence types which can be related to one another.

The individual cyme in *Phyllanthus* is of course a determinate structure with a terminal female flower (if it is bisexual). But in those species with cymes aggregated into a compound inflorescence, the latter is indeterminate; there is never a single flower terminating the main axis as in *Jatropha* or *Euphorbia*. Since it appears that the phylogenetic trend of inflorescence modification in *Phyllanthus* has been one of reduction, the more elaborate types will be considered first.

The species of sect. *Elutanthos* have the least modified kind of inflorescence among the West Indian species and — except for the Australasian sect. *Nymania* — the genus as a whole. Of the species of sect. *Elutanthos* the Mexican *P. grandifolius* has the most elaborate aggregations of flowers. The proximal portion of the floriferous branch (i.e., the branch of the current year) bears normal foliage leaves, some of which subtend thyrses of male flowers. Each male thyse is composed of a number of cymules arranged alternately on the flexuous axis. The male cymules are dichasial only at the very base and monochasial thereafter, so that two or three "pseudo-racemes" of flowers appear fascicled together at one node. The distal portion of the floriferous branch is itself modified into a thyse which only differs from the male inflorescence in that the individual cymules have fewer flowers and thus are more fascicle-like than raceme-like.

*Phyllanthus grandifolius* is interesting not only because of its elaborate aggregations of flowers, but also because it shows in an unspecialized condition the tendencies which lead toward the inflorescences of other

species. For example, two trends occurring in *P. grandifolius* and in many other species are: monochasial development of cymules and production of male flowers proximally relative to the female flowers (on the entire branchlet or thyrse). In *P. grandifolius* the sexes are more or less completely segregated, the male flowers being borne on axes in the axils of normal foliage leaves and the female directly in the axils of the distal leaves, which are usually reduced to bracts. There is thus in this species a striking (though not invariable) correlation between the terminalization of the female flowers and the reduction of the subtending leaves to bracts. This reduction phenomenon may not be taken as a general rule, however, because in other species it is the proximal leaves subtending the male flowers which are reduced. The terminalization of the female flowers, on the other hand, occurs almost invariably whenever the plant is monoecious and the cymules unisexual; only in the few species of sect. *Urinaria* is the order definitely reverse.

The West Indian species of sect. *Elutanthos* differ from *P. grandifolius* in having mostly bisexual cymules and less elaborate inflorescences. The flower arrangement in these, and all the other species with non-phyllanthoid branching, is so variable and dependent on the vigor of the shoot that it is very difficult to write a good taxonomic description of it. In *P. nutans*, for example, the female flowers tend to be clustered in the axils of reduced leaves on a flexuous "semi-naked" axis (more exactly, a racemi-form thyrse), while the male flowers are borne either in clusters axillary to foliage leaves or at the lower nodes of the thyrse. In this, as in all the species of sect. *Elutanthos*, the boundary between the vegetative and fertile zones of the plant is not well defined.

In the herbaceous or subshrubby species of sect. *Paraphyllanthus*, (none of which occur in the West Indies), the cymules are reduced to dense clusters that are always axillary to foliage leaves. The flower-clusters are extremely variable, at least in the widespread *P. polygonoides*, which may be either monoecious or dioecious and which may have both unisexual and bisexual cymules on the same individual. Furthermore, branch buds may be produced at the same axil as a flower cluster.

The three West Indian species of sect. *Loxopodium* have a similar sort of floral arrangement, and branch-buds may similarly be produced at the same axils with the flowers; but usually the arrangement of the sexes is much more definite as to number and position. The cymules may contain from one to five female flowers and as many male, but the inflorescence axis is always so greatly contracted that it is not evident to casual inspection. There thus appears to be no fundamental difference between the pattern of flower production in the various sections with non-phyllanthoid branching; flowers may be produced (at least potentially) at any node on any axis (except possibly for the lowermost nodes on the seedling axis).

In the remainder of the West Indian species, however, as well as in the majority of those in the entire genus, the flowers are borne only on deciduous branchlets and never on the main axis or on permanent branches. Among these West Indian species with phyllanthoid branching, *P. juglandi-*

*folius* displays relatively unspecialized inflorescences. The cymules are mostly bisexual, and those of the proximal axils of a branchlet often have three or four female flowers accompanied by several males; the number of female flowers decreases distally until the cymules at the tip of the branchlet are entirely male. In a few other species such as *P. discolor* there may be two or three female flowers per cymule, but in most species there is only a single female flower and the cymules are often unisexual. *Phyllanthus juglandifolius* is exceptional not only in its relatively elaborate inflorescences, but more especially in its tendency toward proximal production of female flowers, which is exactly the reverse of the trend in most other species.

Perhaps the most striking evolutionary trend is apparent among the herbaceous species with phyllanthoid branching, in which there is a very evident shift from bisexual to unisexual inflorescences. With the exception of the anomalous *P. elsiae* there are no woody American species of *Phyllanthus* which are dioecious; but in a number of the herbaceous species of sect. *Phyllanthus* entire plants, as well as individual cymules, may be unisexual. However, even in these species the dioecious condition is not absolute, for male branchlets will occasionally produce one or two female flowers at the tip, and while female branchlets never produce any male flowers (at least in the West Indian species) a female plant may produce a few male branchlets. In contrast to this imperfect dioeciousness in *Phyllanthus*, the West Indian representatives of the related genera *Astrocasia*, *Flueggea*, *Savia*, and *Securinega* appear to be completely dioecious.

In most of the herbaceous species of sect. *Phyllanthus* the combination of the trends toward unisexuality of cymule and terminalization of female flower has resulted in branchlets with proximal cymules of several male flowers and distal cymules each of a solitary female flower. The common weedy species *P. amarus* is exceptional in that it has bisexual cymules, each with one male and one female flower.

In a few species the reduction of the cymule has proceeded to the point where it is composed only of a solitary flower. This situation prevails in the herbaceous species of sects. *Callitrichoides* and *Cyclanthera* and in several shrubby species of sect. *Orbicularia*. Among the latter, however, the condition is not as strongly fixed, for occasionally paired flowers may be produced on a branchlet which otherwise has only solitary ones.

The West Indian species with bipinnatifid branchlets have a special sort of distribution of flowers. In *P. subglomeratus* and many of the South American representatives of sect. *Nothoclema* cymules are produced at all the nodes of both the ultimate and penultimate axes. In the other West Indian species of *Nothoclema*, *P. acuminatus*, flowers are likewise produced at all the nodes of the ultimate axes; but on the penultimate axis there are cymules only at the proximal nodes which do not subtend ultimate axes, and sometimes there are no floriferous nodes on the penultimate axis. In the species of sect. *Hemiphyllanthus* this "sterilization" is complete and flowers are produced only on the ultimate axes.



In the section on growth form the origin of cauliflory in *Phyllanthus* has been ascribed to the modification of floriferous branchlets to "naked" thyrses with the leaves reduced to scales and to the production of these modified branchlets in fascicles at nodes of the previous year's growth. It is probable that among the species represented in the West Indies, cauliflory has arisen independently at least twice: in sect. *Cicca* and in sect. *Epistylum*. The basic prerequisite for cauliflory is of course the reduction of the leaves subtending the cymules; but in *Phyllanthus* there is evidently not a very strong trend in that direction. It is true that in a great many species the proximal leaves of a branchlet are often smaller than the distal ones and subtend male cymules; this suggests that there may be some nutritional effect on both the expression of leaf size and sex of flowers. But on the other hand there are a number of species in which the correlation is reversed and it is the distal leaves subtending the female cymules which are reduced. This diversity in sex expression and leaf modification raises some interesting physiological problems. The species with phyllanthoid branching would seem to be promising experimental plants for research in sex determination such as that carried out by Nitsch et al. (1952) on the Cucurbitaceae. These authors showed that sex expression in the cucumber may be controlled by varying temperature and light, at least to the extent of modifying the number of nodes bearing a particular kind of flower. Similar experiments carried out with the view of comparing the response of a species of sect. *Urinaria* (with female flowers proximal on the branchlet) and a species of sect. *Phyllanthus* (with the female flowers distal) might yield significant results.

Croizat (1943, 1944) has discussed the morphology and evolution of inflorescence in *Phyllanthus* and has suggested a different interpretation from that adopted here. In his first paper he asserted:

"In certain groups of *Phyllanthus* true leaves are present, the floriferous axes being often reduced, bracteate, and, strictly speaking, leafless branchlets (see *P. laxiflorus* [*P. grandifolius*]). In other groups of the same genus the true leaves are represented only by scales, the aspect and function of foliage being assumed by the bracts of the floriferous axes (see *P. mexiae*)."

In his fuller account the following year it is evident that Croizat's view of the evolution of inflorescence in *Phyllanthus* is based on two main assumptions: first, that the solitary axillary flower represents the primitive type of inflorescence, and second, that the foliage leaves of species with phyllanthoid branching represent bracts which have presumably been "de-differentiated" into leaves. Majumdar and Arshad Ali (1956: 158), on the basis of their studies of *P. amarus* and *P. reticulatus*, have come to a similar conclusion as regards the latter point. Because the buds in the axils of the leaves of the branchlet produce only flowers, they suggest that the branchlets of these two species should be called inflorescences and the leaves should be called bracts.

The term *anthocladium* has been applied by Goebel (1931) to a branch in which the determinate (i.e. cymose) branching pattern of the inflores-

cence is superimposed on the indeterminate pattern of the vegetative shoot. In *Phyllanthus*, as specifically pointed out by Goebel (1931: 22), the floriferous axis is monopodial and thus cannot strictly be termed an anthocladium. Nevertheless, it is very evident that in *Phyllanthus* the fate of the deciduous branchlet is intimately related to flower production.\* But to call either the anthocladium of *Euphorbia* subg. *Chamaesyce* or the deciduous branchlet of *Phyllanthus* an "inflorescence" is not only unwarranted but holds the danger of introducing confusion in terms. In all the species of *Phyllanthus* investigated, the leaves subtending the cymules are typical foliage leaves indistinguishable (except sometimes by a minor difference in shape) from those on the seedling axis. If one were to follow Croizat and Majumdar in calling the branchlet leaves "bracts", this would contradict the classical definition of the latter term (cf. Gray, 1879: 118), which definitely requires a bract to show a difference in form. Furthermore, neither in *Phyllanthus* nor in *Euphorbia* subg. *Chamaesyce* is there any evidence that the leaves associated with the flowers or cyathia have metamorphosed back from bracts.

#### FLOWER

Few other genera of angiosperms display a range of variation in flower structure comparable to *Phyllanthus*, even when such divergent groups as *Astrocasia* and *Margaritaria* have been removed from it. It is not surprising, therefore, that during the first half of the nineteenth century many small genera justified by "technical" floral characters were erected on various species now included in *Phyllanthus*. One of Mueller's greatest accomplishments was his perception of the essential similarity between these many small "genera", and his synthesis of these fragments into a unified and—on the whole—natural generic concept. In placing *Glochidion* within the confines of *Phyllanthus*, Mueller emphasized the relationship of these two groups in floral morphology, and Hooker implicitly recognized this when he had to justify the resurrection of *Glochidion* chiefly on the grounds of convenience.

Floral diversity is enhanced in *Phyllanthus*, as in other genera of the Euphorbiaceae, by virtue of the fact that the male and female flowers have often evolved in different ways. But at the same time there has been in both sexes a trend towards reduction of number of parts, accompanied by a decrease in variability. The structural differences between the male and female flowers in the various species may be ascribed to the interaction of two factors: the duration of the flower (the male being relatively fugacious) and the difference in the number of sporophylls. It appears that in some instances the number of calyx-lobes developed in the mature flower is affected by the shape of the androecium or gynoecium primordium during development. Thus in an appreciable number of the species which

\* From a dynamic point of view it might be worth while to broaden the definition of "anthocladium" to include highly specialized monopodial branches which behave as inflorescence-units.

have male flowers with only two stamens the calyx-lobes of the male flower are reduced from five to four, whereas the female flowers still have five calyx-lobes.

The flowers of *Phyllanthus* are exclusively unisexual, and ordinarily there is no trace of the organs of the missing sex. Section *Cicca* is the only group in which definite staminodes occur; and these may even produce a few pollen grains, though it is not known if any of these "female" pollen grains are fertile. From time to time various authors have described species of *Phyllanthus* with a "pistillode" in the male flower, but on close examination this structure has always proved to be the apiculate tip of the staminal column, which may represent either an abortive stamen or one or more prolonged anther connectives. Any "Phyllanthus-like" plant which does have a pistillode may confidently be referred to some other genus.

The floral biology of *Phyllanthus* remains an almost uncharted area, partly because so many of the species grow in localities where protracted field observation is difficult. The great diversity in flower structure suggests specialization for different types of insect visitors, but almost nothing is known of how any of the species are pollinated. Personal observation in Cuba of the pollination of *P. dimorphus* by chrysomelid beetles (unfortunately not further identified) and of *P. orbicularis* by bees has given the merest glimpse into the pollination relationships of the genus.

### Pedice! and Torus.

The pedice! of the male flower is terete, usually slender, and is about as long as or longer than that of the female flower. This proves to be a good, albeit superficial, character for distinguishing *Phyllanthus* from related genera such as *Savia* and *Securinega*, where the male flowers are mostly sessile and the female flowers long-stalked. In a few species of *Phyllanthus* (e.g., *P. tenellus*) the pedice! of the female flower is much longer than that of the male, but usually it is shorter and in some species such as *P. urinaria* is shortened to scarcely more than a broad platform beneath the calyx.

Histologically, the pedice! is usually rather simple. The epidermis (in the proximal portion, at least) lacks stomata and is composed of cells with rectangular outlines. A "hypodermis" may sometimes be distinguished, at least in the base of the pedice!, by the tannin content of the subepidermal layer. In all of the male flowers examined, sclereids are completely absent, the axis of the pedice! being occupied only by a few slender tracheids. The female flowers of many species likewise have only tracheids, but the pedice! of *P. niruri* shows a very characteristic sclerification. Towards the base of the pedice! slightly elongated "brachysclereids" occur around the outside of the vascular bundle; these become progressively longer distally but stop about halfway up the pedice!. Beneath the brachysclereid layer, however, is a layer of fibers which run to the very top of the pedice!



and end in the receptacular region. It is very curious that some of the woody species examined, although having much larger fruit than *P. niruri*, entirely lack fibers or sclereids in the pedicel. Crystals are typically much less numerous in the pedicel proper than in the receptacle or ovary.

The top (distal) portion of the pedicel is expanded (sometimes abruptly) into a receptacle which merges with the basally fused calyx lobes so that it is neither conspicuous nor clearly defined. In the female flower the upper portion of the pedicel may gradually (as compared with the male) enlarge up to the toral region, and in some of the species of sect. *Hemiphyllanthus* this dilated portion may become large and fleshy. The enlargement reaches such grotesque proportions in the female flower of *P. megapodus* that the expanded pedicel-receptacle is larger than the rest of the flower. In *P. subcarnosus* the expanded portion of the pedicel contains chlorenchyma.

The pedicel characteristically hangs so that the male and female flowers project below the plane of the leaves on the branchlet. After the fertilization period the pedicel of the male flower disarticulates, but that of the female flower remains relatively unchanged. During the development of the fruit the pedicel may elongate slightly, but (at least in the West Indian species) the increase in length is never very great.

### Calyx.

The flowers of *Phyllanthus*, in common with those of most of the Euphorbiaceae, are apetalous with a gamophyllous calyx. The union of the calyx-lobes at the base is sometimes slight but almost always noticeable on close inspection, and except in very rare instances (e.g., *P. subcarnosus*) they never disarticulate separately from the receptacle. In many species the calyx, as if in compensation for the lack of petals, is petaloid and conspicuous, red or pink (and more rarely purplish) being the prevailing hues; and the disk is often of a contrasting color. In other species, particularly the herbaceous ones, the calyx is yellowish or whitish, and in a few the female calyx is green and foliose.

As suggested by Michaelis (1924) for the Euphorbiaceae as a whole, the basic arrangement of the calyx-parts in *Phyllanthus* appears to be five lobes in imbricate aestivation; four lobes in decussate pairs or six in two whorls represent derived conditions. The number of lobes may vary within the same species, and does not necessarily correspond between the male and female flowers. Although the male and female calyces of some species are very similar, the female calyx is very often larger, stouter, and composed of a greater number of lobes.

Usually each calyx-lobe of the male flower has a single unbranched or sparsely branched vein; in the latter case, the branch-tips, of more or less enlarged tracheids, occur flabellately near the tip of the lobe. In species with fairly massive male flowers, such as those of sect. *Thamnocharis*, there may be three parallel sparsely branching veins. The calyx of the female flower usually has more elaborate venation than that of

the male. In sect. *Paraphyllanthus* (which is not represented in the West Indies) the female calyx-lobes are quite green and foliaceous; the mid-vein branches much as in the leaf to form a reticulate pattern, and the interior of the lobe is occupied by chlorenchyma. The calyx-lobes of the species in this section are more leaf-like than those of any of the West Indian species, which have no well-defined chlorenchyma. However, stomata occur on the epidermis of the female flowers of many species and rarely even on the epidermis of the male (e.g., *P. ekmanii*). Reticulate venation is not well-developed in the calyx-lobes of any of the West Indian species, but in the lobes of species with massive female flowers (such as in sect. *Thamnocharis*) there are instead a number of parallel veins conspicuously jacketed with fibers.

The texture of the calyx varies from thinly herbaceous to coriaceous among different species; the margins even of the coriaceous lobes are thin, and sometimes are denticulate or lacerate. At anthesis the calyx-lobes of both male and female flowers are usually more or less spreading, but in some species the lobes of the female calyx remain erect and imbricate around the ovary. The female calyx remains relatively unchanged during maturation of the fruit except that sometimes the lobes become reflexed. *Phyllanthus subcarnosus* (sect. *Omphacodes*) is exceptional in that the female calyx-lobes are very early deciduous from the receptacle.

#### Disk.

The term *disk* as used here refers to the more or less glandular mass of tissue arising from the receptacle between the calyx and the androecium or gynoecium. In *Phyllanthus* the disk is invariably outside the stamens; but the situation is reversed in some other genera of Phyllanthaceae such as *Drypetes* and *Reverchonina*. In the male flower the disk is ordinarily divided into segments isomerous and alternating with the calyx-lobes. The disk-segments are often closely contiguous and they may be united in pairs or all united into a continuous saucer- or cup-shaded disk. A few species such as *P. emblica* have male flowers with the disk reduced or absent, and in *P. elsiæ* the disk is absent in both sexes; the latter situation prevails in other genera of the Phyllanthinae such as *Glochidion* and *Breynia*. In the female flower of *Phyllanthus* the disk is most commonly continuous, and only in a rather small number of species is it divided into segments like the disk in the male flower.

The term *disk-segment* as used here is synonymous with the "disk-gland" of most authors. The latter term is unwieldy because there are some species of *Phyllanthus* in which the disk-segment is itself provided with glands. The disk-segment is more or less equivalent to the "nectary," but the latter term suffers from the ambiguity that it is sometimes applied to the entire disk of a flower and sometimes to the individual disk-segments. It must be kept in mind that the disk-segment is a topographical designation and is not intended to convey any developmental implications. The disk does not necessarily begin development as an entire structure and then break up into segments, either in ontogeny or phylogeny.

The disk may be greenish, yellowish, pink, or even deep red or purple when fresh, but on drying it usually loses its distinctive color and becomes brownish. In many species the disk-segments are crenulate or lobed and appear pitted under high magnification. Microtome sections show that in *P. reticulatus*, for instance, there is a stoma at the bottom of each of the well-like pits, and that the cells making up the disk are smaller and have denser cytoplasm than those in most of the other floral parts (PLATE-FIG. 46). Stomatal pits have been observed in the disk of most of the species studied from paraffin sections, and in some species (e.g., *P. ekmanii*) they can be easily seen in cleared whole mounts. This histological evidence leaves little doubt that the disk of *Phyllanthus* is a true nectary in function. The amount of nectar secreted by the disk is evidently small in most species, since the disk of flowers examined in the field usually appears merely moist. A considerable quantity of nectar has been observed only in *P. polygonoides*, an extra-Caribbean species. The flowers of most species appear to be quite odorless, but it has been reported that the common *P. epiphyllanthus* has flowers which give off an evil smell at night.

Many species have flowers with a relatively massive disk in one or both sexes. The Indonesian species *P. ceramanthus*,\* with both the androecium and gynoecium almost completely enclosed in an urceolate disk, represents the extreme in vertical extension. *Phyllanthus emblica* has the most disparate disk structure in the two sexes of any species examined; the female disk is a cup like that of *P. ceramanthus* and with a lacerate rim, but the male is reduced or absent. The West Indian *P. chryseus* is of especial interest, not only because it has the relatively largest disk of any species examined, but also because of the vascular supply to it (PLATE-FIG. 45). In species such as *P. reticulatus*, which have a much smaller floral disk, there is no sign of a special vascular supply. This suggests that in *Phyllanthus*, at least, vascularization of the disk is a function of size and can have no particular significance for purposes of homologizing different parts of the flower.

The question of the morphological nature of the disk in the Euphorbiaceae is of some theoretical interest and has been discussed by a number of workers. Baillon (1858) clearly distinguished between staminode and disk; he regarded the latter as an expansion of the torus on the basis of his ontogenetic studies. His view is clearly shown in his discussion of the hypogynous glands of *Cluytia pulchella*:

"Quant aux cinq glandes bilobées de la fleur femelle, elles constituent un vrai disque, et l'on peut suivre facilement . . . son développement ultérieur a celui du pistil. Si c'étaient des staminodes, elles apparatraient avant lui."

Baillon's assumption that there is a perfect correlation between the morphological nature of floral organs and the time of their initiation in development is bound to be suspect in this sceptical age. Michaelis (1924: 113), on the basis of his own studies on the Euphorbiaceae, does not con-

\* *Phyllanthus ceramanthus* nom. nov.; *Ceramanthus gracilis* Hassk. Cat. Hort. Bogor. Alt. 240. 1844; non *Phyllanthus gracilis* Roxb. Fl. Ind. 3: 655. 1832.



sider the delayed appearance of the disk a proof against its staminodial origin. He found that in *Croton* and *Codiaeum* rudimentary calyx- and corolla-parts were delayed in ontogeny, and concluded therefore that the late appearance of the disk may likewise be only an indication of its rudimentary nature. The entire problem appears to need reinvestigation; but in any event, ontogenetic studies of *Phyllanthus* — in which the disk always appears very late — do not seem likely to provide decisive evidence.

Eichler, in his "Blütendiagramme" (1875: 4, 48–49) regarded the disk in most angiosperms as representing an emergence of the axis (specifically, the receptacle). In addition to remarking on the belated development of the disk, he added the important generality that the disk structures do not alter the arrangement of whorls in the flower and therefore cannot represent an independent cycle. Bentham and Hooker (1880: 239), Pax (1890: 1) and Pax and Hoffmann (1931: 13) followed Eichler's conception in interpreting the disk in the Euphorbiaceae.

A different interpretation has been presented by Michaelis (1924), who in a vigorous refutation of the "emergence" theory has suggested that the disk-structures of the Euphorbiaceae are mostly derived from reduced stamens. His argument is based on a number of his observations: (1) the regularity of position of the "Diskusdrüsen," which occupy the positions of the outer staminal whorl; (2) the resemblance of the disk-segments of *Chiropetalum*, *Cluytia*, et al., to immature stamens; (3) the development of "archesporial tissue" in the disk-segments of *Erythrococca*; (4) the occasional replacement of "disk-glands" by stamens; and (5) the lack of appreciable nectar or sugar content in the disk.

In the present study Michaelis's viewpoint has been considered only as it relates to the Phyllanthaceae, and no attempt has been made to check his observations on members of the Crotonoideae. A detailed reading of his work shows that he depended heavily on evidence from the polyandrous species of *Croton*, in which the disk-segments alternate with the petals and thus occupy the position of an outer staminal whorl. However, at least in the more primitive genera of Phyllanthaceae the disk-segments (where separate) are definitely opposite the petals and can scarcely represent an abortive outer staminal whorl. Furthermore, in the occasional hermaphroditic flowers of *Phyllanthus acidus*, the staminodes appear in addition to the normal hypogynous disk; in this species, therefore, there can hardly be any doubt that the disk is not staminodial in origin.

It is difficult to understand Michaelis's contention that the disk does not play a rôle as a nectary. It is true that, as he asserts, there is no evident amount of free nectar in the flowers of many Euphorbiaceae. But in *Phyllanthus*, at any rate, the anatomical structure of the disk shows that there can be little doubt of its secretory nature. The pendent male flowers of most species of *Phyllanthus* are furthermore hardly capable of holding any sizeable quantity of nectar.

Evidently Michaelis, in drawing up his "staminodial" theory of the disk, has leaned too strongly on evidence from the Crotonoideae. Baillon's ex-

PLICIT statement (1858: 127) that there are never any staminodes in the female flower of the Phyllanthoideae appears to be essentially correct (excepting *Phyllanthus acidus*). If Michaelis's observations of the Crotonoideae are correct, then it would appear that the disk in that subfamily is by and large not homologous with that in the Phyllanthoideae. Further research must be done in the Crotonoideae to reconcile the conflicting accounts of Michaelis and Baillon.

If the possibility of staminodial origin of the disk in *Phyllanthus* is rejected, the "emergence" theory remains to be examined. It is quite possible, as Baillon and Eichler suggested, that the disk is purely an expansion of the torus, as it appears to be in such families as the Cruciferae. However, the striking topographical arrangement of the disk-segments suggests another possibility. In the genera of Phyllanthae in which a corolla is developed (e.g., *Andrachne*, *Astrocasia*) the disk-segments are opposite the petals, not alternate as they would be if they represented the outer staminal whorl. In *Phyllanthus*, where the corolla is absent, the disk-segments (if free) occupy the same relative position as the missing petals (i.e., alternate with the calyx-lobes). This suggests that the disk may belong to the corolline whorl. In *Andrachne* and some of the primitive species of *Phyllanthus* (e.g., *P. polygonoides*) the disk-segments are more or less bifid (cf. Michaelis, pl. 1, fig. 1). Their appearance and antepetalous position suggests that the disk-segments in these plants may be "ligular" appendages of the petals corresponding to the "Nebenkrone" of the Caryophyllaceae. The production of glandular appendages by the floral leaves can hardly be considered remarkable in a family such as the Euphorbiaceae, where glandular structures are commonly associated with the basal portions of foliage leaves and bracts. Nor can the usual lack of vascular supply to the disk be considered surprising when it is recalled that the suppressed petals have left no rudimentary vascular traces either. However, at present it is really not possible to decide whether the disk-segments should be considered toral expansions or corollar appendages; the simple structure of the disk does not offer any clues definite enough to choose between the two alternatives.

### Androecium.

According to Michaelis (1924: 121) the primitive androecium in the Euphorbiaceae is one of many stamens in several whorls; he found no evidence of phylogenetic increase in stamen number except in a few anomalous cases such as *Ricinus*. In *Phyllanthus* reduction from a polymeric androecium to one with few stamens may be traced in at least two phylogenetic lines, one of which is in the West Indies. *Phyllanthus discolor* (sect. *Williamia*) has ten to fifteen stamens with the filaments connate and the anthers spirally disposed or in three whorls; this is the highest stamen number found in any New World species. *Phyllanthus microdictyus*, the other species of sect. *Williamia*, has six to ten stamens in two or three whorls (the filaments being connate in all these related species). In sects. *Williamiandra* and *Orbicularia*, which are clearly derived from sect.

*Williamia*, the stamen number is mostly six, but in *P. phlebocarpus* of the latter section it is reduced to three. There can be little doubt that these species are related and that there has been a progressive reduction in stamen number during the evolution of the group. However, sect. *Williamia*, because of its phyllanthoid branching and areolate pollen grains, cannot be one of the most primitive groups in the genus. Furthermore, in sect. *Elutanthos*, which appears to be the progenitor of *Williamia*, the stamens are never more than three; and this small number also characterizes the vegetatively primitive species of sect. *Paraphyllanthus*.

Section *Polyandroglochidion* of New Caledonia, with up to fourteen stamens, is the only other group with over ten. In this group the pollen grains are colporate and the stamens free, but vegetatively the representatives have the specialized phyllanthoid branching. On the basis of the existing species of *Phyllanthus*, therefore, it would appear necessary to postulate an increase in stamen number from the three to five of primitive sections like *Paraphyllanthus* and *Menarda* to the ten or more of *Williamia* and *Polyandroglochidion*. That this is not impossible is apparent from the fact an undoubted increase in carpel number has occurred in a few cases. However, another and perhaps more likely possibility is that the various groups of *Phyllanthus* are descended from an ancestor — now extinct — which had a polymerous androecium combined with unspecialized branching. Evolution of the living representatives of *Phyllanthus* from such an ancestor would render unnecessary any hypothesis of increase in stamen number.

In the vast majority of the species of *Phyllanthus* the stamen number is six or less. Androecia of two, three, or four stamens have doubtless evolved by reduction from hexamerous and pentamerous ones such as those of sects. *Chorizandra* and *Anisonema*, respectively. More or less concomitant with reduction in stamen number are the two tendencies toward: (1) coalescence of stamens, at first by the filaments and then by the anthers; and (2) displacement of the line of anther dehiscence from vertical to horizontal.

Among the West Indian species, the introduced *P. tenellus* has the least-modified androecium, of five free stamens. In sect. *Cicca* there are four free stamens, and in sect. *Loxopodium* three. In the rest of the sections (except in relatives or descendants of sect. *Williamia*) there are either two or three stamens which are usually connate. In the most highly evolved androecia the anthers are oriented so that the line of dehiscence is horizontal and in sect. *Epistylum* they are deflexed so as to appear upside down.

Mueller depended heavily on these differences in stamen number and direction of anther-slits in distinguishing sections of the genus. Bentham (1878) rightly criticised this as leading to an unnatural classification; but Mueller was not unaware of the artificiality of the dehiscence character. The use of anther characters appears to have been largely a matter of expediency on the part of Mueller. Unfortunately for those who have subsequently had occasion to consider the subgeneric classification of



*Phyllanthus*, this character has proved to be a poor choice not only because of the violence it does to relationships but also because of its ambiguousness. Baillon (1858: 112) had already observed: "Je ne connais pas chez les Euphorbiacées, quoi qu'en disent quelques descriptions, d'exemples positifs de dehiscence transversale." As Baillon realized, the anthers in *Phyllanthus*, as in other Euphorbiaceae, nearly always open longitudinally with respect to their own axes; most "transversely dehiscent" anthers merely have been bent onto the horizontal plane without the line of dehiscence changing relatively to the long axis of the anther. Nevertheless, there is in some species at least a partial displacement of the dehiscence-plane; the slits of the anther sacs, instead of being perfectly parallel, come together on the abaxial face and are confluent in a single arc. This type of dehiscence may be truly "oblique" but in practice the distinction is excessively subtle. The reader of the descriptions in this work may assume that the anthers open by slits that are longitudinal or nearly so, and that the stated direction of dehiscence will apply in relation to the long axis of the flower rather than to the anther itself.

The final product of the trend towards reduction and coalescence of the stamens has been reached in those species of *Phyllanthus* in which the stamens with horizontally dehiscing anthers are completely fused, so that the androecium presents the appearance of a single stamen with a peltate anther that dehisces all the way around the circumference. This remarkable compound structure, or *synandrium*, characterizes all the species of the West Indian sect. *Cyclanthera* and occurs also in the Cuban *P. dimorphus* and in two species of Madagascar (Leandri, 1938). Personal examination of the Madagascarian *P. ivohibeus* has shown that this species, like *P. dimorphus*, belongs to sect. *Phyllanthus*. Possibly these two species are related so that the synandrium evolved only once within sect. *Phyllanthus*. But in any event the synandrium must have developed independently in the very different sect. *Cyclanthera*. Since many species of *Phyllanthus* have an androecium of three stamens with the anthers sessile atop a column, the independent origin of the synandrium can actually be accounted for rather easily on mechanical grounds; all that is required is fusion of the connectives and coalescence of the anther-slits.

The study of the androecium for taxonomic purposes, i.e., with the intention of finding "key" characters, is attended with the difficulty that the filaments are very late in developing. The conspicuous staminal column of the mature male flower may be scarcely evident in the bud, and stamens which actually are connate by the filaments may be interpreted mistakenly as free. This rapid expansion during anthesis also characterizes the styles of many species and should be kept in mind by anyone who is drawing up or attempting to use a description.

Anatomically the stamens of *Phyllanthus* offer little of interest, at least in the forms which have been investigated. Each stamen is supplied with a single trace of slender tracheids which in the connective may bifurcate or end entire. The traces of the individual stamens remain separate in the staminal column. The anthers, unlike those of many other Euphorbi-

aceae, have no special vesture or glandular development. The connective undergoes a number of modifications, being enlarged and emarginate between the anthers in some South American species and apiculate in several Old World species; but in our West Indian representatives it is unspecialized.

### Pollen grains.

One of the most striking discoveries made during the study of the West Indian species of *Phyllanthus* was the extraordinary diversity of pollen morphology within the genus. Erdtman (1952) reported for the first time the characteristic pollen grain of subg. *Xylophylla*; but by a curious circumstance, all of the four species he reported on happened to have areolate grains, and he apparently was unaware of the great intrageneric variability. During the present study the pollen of about one-third of the species in the genus has been examined, including many Old World species and at least one species from all except one or two sections. Although a number of phylogenetically critical species have so far not been investigated (due to lack of material), the general lines of pollen morphology within *Phyllanthus* are now apparent.

Erdtman's general discussion of pollen morphology and his special treatment of the Euphorbiaceae have provided much assistance and stimulation during examination of the pollen of *Phyllanthus*. However, his very complex terminology appears not only unwieldy but also needlessly complicated as far as the needs of systematists, rather than palynologists, are concerned. Much of the terminology in the following discussion has consequently been adopted from that proposed by Faegri and Iversen (1950).

The small size of the microspores of *Phyllanthus* is doubtless partly responsible for their being so poorly known. They average around  $20\mu$  in diameter, and grains over  $30\mu$  broad are rare. Observation under an oil immersion lens is usually necessary to determine the ornamentation pattern of the exine. The use of pollen characters is therefore not practicable for routine determinations; but it is an invaluable aid in assigning species to their place within the genus.

The commonest and probably the basic type of pollen grain in the Phyllanthoideae and some of the tribes of Crotonoideae much resembles those in such families as the Flacourtiaceae, Sapindaceae, and Celastraceae. It is subglobose or broadly ellipsoidal and thin-walled, with a reticulate exine. In most cases the reticulum is sharply defined and raised, so that the ornamentation of the exine falls into the "OL" pattern of Erdtman (1952: 22), i.e., the spaces between the walls (muri) of the reticulum are dark at the outermost focus and bright at the inner focus. In the grains of many species of *Phyllanthus* the reticulum is so fine that it can scarcely be resolved even under oil immersion. The exine is provided with three longitudinal furrows (colpi) which usually have median round or elliptic germ-pores (ora). Both Erdtman and Faegri and Iversen have applied the term "tricolporate" to grains of this type.

Tricolporate pollen grains are characteristic of the presumably primitive petaliferous genera of Phyllanthaceae such as *Andrachne* and *Savia*, and of the apetalous genera more closely related to *Phyllanthus* such as *Securigena* and *Flueggea*. In *Phyllanthus* such grains occur in a number of groups, including sects. *Paraphyllanthus* and *Phyllanthus* (PLATE-FIG. 35). In several species, including those of sects. *Loxopodium*, *Urinaria*, and part of sect. *Phyllanthus*, the microspore is very similar except that there are four colpi instead of three. *Phyllanthus niruri* (PLATE-FIG. 34) has unusually large prolate grains which (like some other species of sect. *Phyllanthus*) have a "heterobrochate" exine, the reticulum being much coarser midway between the colpi than along their margins. In most species, however, there is no such striking difference in the fineness of different parts of the reticulum.

The majority of the species native to the West Indies have a type of pollen grain very different from that just discussed. It was illustrated by Erdtman (1952: fig. 97a) and described by him as "synrugoidorate," i.e., "provided with rugoid streaks surrounding angular (usually 5-angular) areoles." In the present work these grains will be referred to as "areolate" (PLATE-FIGS. 41 & 42). All such grains are spherical and quite similar in ornamentation, differing mainly in size and in the number of areoles. At each corner of the areole, where three furrows come together, is a circular germ-pore. There is a distinct and continuous exinous ridge which bounds the perimeter of the areole and at the same time defines the edge of the furrow; it is formed by the amalgamation of the minute club-shaped sculptural elements of the exine ("pila" of Erdtman, "clavae" of Faegri and Iversen). Within the areole, the clavae form a reticulum which is very much like that of ordinary colporate grains.

Areolate pollen grains of the kind just described are known only from New World species of *Phyllanthus*. However, areolate grains that superficially are very similar occur in the Old World species of sect. *Macraea*; Erdtman, in fact, noted no essential difference between the grain of the West Indian *P. mimosoides* and the Hawaiian *P. sandwicensis* [= *P. distichus*]. But close examination shows that in the latter the ora are located midway between the angles of the areoles and thus in the middle of one furrow rather than at the intersection of three of them (PLATE-FIG. 43). A similar kind of pollen grain occurs in the Indo-Chinese species *P. ruber*, whose affinities are rather doubtful. From various lines of evidence it is clear that the Old World species with areolate grains are not closely related to the New World species; apparently the areolate ornamentation has evolved quite independently in the two groups.

A third kind of areolate microspore occurs in the West Indian sect. *Cyclanthera*. It resembles the other two except for the fact that the reticulum within the areole is reduced to a single brochus. The areole therefore appears to have a median pore (or plug, depending on the plane of focus) and may be referred to as "foveolate" (PLATE-FIG. 40). It is evident from various considerations that sect. *Cyclanthera* is derived from



sect. *Callitrichoides*, and that its foveolate grain must be derived from the grain of the latter, which has ribbon-shaped areoles that give the exine a striate appearance (PLATE-FIG. 39). It is at present impossible to be sure if the "banded" grain of sect. *Callitrichoides* is derived from the areolate grain of other West Indian species. It might have evolved independently; but the relationships of sects. *Cyclanthera* and *Callitrichoides* are too obscure to decide the matter.

There are a number of other kinds of pollen in *Phyllanthus* which fall into neither the areolate nor the ordinary colpate type. In sect. *Nothoclema*, for instance, the colpi are greatly shortened to dumbbell-shaped furrows with a germ-pore at each end, and the exine is markedly echinulose ("pilate" in Erdtman's terminology) (PLATE-FIG. 36). The spherical grain of the introduced *P. pulcher* (sect. *Eriococcus*) has no evident furrows, or areoles, and the reticulum is broken only by equidistantly placed pores (PLATE-FIG. 44).

The diversity of pollen types in *Phyllanthus* is thus so great that it becomes difficult to interpret the possible evolutionary relationships between the different kinds. Erdtman has designated as "breynioid" the pollen occurring in the "subtribes" Glochidiinae, Phyllanthinae, and Sauropodinae. As found in *Breynia* the pollen grain is more or less oblate with several (7 to 10) furrows, each having two ora, and a prominent reticulum set off from the furrow by a definite border. Well-marked breynioid grains have been observed in *Phyllanthus* only in the South American species of sect. *Microglochidion* (PLATE-FIG. 38). However, there is no sharp dividing line between breynioid and ordinary tricolpate grains; in *Glochidion*, for instance, the few species investigated have four-colpate grains which hardly differ from those of many species of *Phyllanthus*.

Erdtman (op. cit. 174) has attempted to relate the breynioid grains of *Breynia* and *Sauropus* to the 4-colpate grains of *Glochidion* on the one hand and to the "synrugoidorate" grains of *Phyllanthus* on the other. This idea has been confirmed, in a general way, in the present study. In sect. *Anisonema* (e.g., *P. reticulatus*) and several Old World groups, the microspore has three colpi which are conspicuously margined and confluent at the poles. If the number of colpi should be increased to five or six and their intersection at the poles be precluded by spatial conditions, the colpi might terminate instead at the margins of the two polar areoles thus formed. The result might be a pollen grain with relatively few large areoles, such as that of *P. subcarnosus* (PLATE-FIG. 41). Further specialization might lead on the one hand, by multiplication of the number of areoles, to the "poly-areolate" grains of many West Indian species, and on the other hand, by suppression of the furrows, to the porate grains of sect. *Eriococcus*. The areolate grain is thus nothing more than a breynioid grain with lateral connections at the ends of the furrows.

Erdtman's suggestions as to the morphological relationships of the pollen grains within the Phyllanthinae thus appear to be sound; but his speculations as to the origin of the "crotonoid" grain are less fortunate. He suggests that the polygonal pattern underlying the "crotonoid" ornamentation

of the grains of *Suregada zanzibarensis* indicates derivation from phyllanthoid pollen. According to this view, the grain of *Suregada* represents a transitional stage between that of *Phyllanthus* and that of *Croton* or *Jatropha*. It is very hazardous, however, to attempt to relate the microspores of genera as far removed as *Phyllanthus* and *Croton*; there is scarcely the slightest possibility that the latter genus is descended from the Phyllanthinae. It appears far more likely that crotonoid pollen grains have been derived from tricolporate types within the Crotonoideae. It is plain from the results of the present study that since very different pollen types may exist within closely related groups, comparisons between widely separated genera in a family such as the Euphorbiaceae are very liable to be unsafe.

### Gynoecium.

The majority of the species of *Phyllanthus* have the typical euphorbiaceous gynoecium of three united carpels, and in common with all the Phyllanthoideae have a pair of collateral ovules in each locule of the ovary. In a few species, none of them native to the New World, the number of carpels is higher. The commonly cultivated *P. acidus* has a variable carpel number, fruits with three and with four locules being almost equally common. In sect. *Anisonema* the number fluctuates from three to ten, and Mueller (1866: 344) reported up to twelve locules in *P. reticulatus* (PLATE-FIG. 47). Otherwise, gynoecia with more than three carpels have been reported only in *P. ruber* (sect. *Nymphanthus*) and *P. buxifolius* (sect. *Scepasma*). It seems significant that the greatest variability in carpel number is concentrated in the single section *Anisonema*. Since the flowers in this section are otherwise basically pentamerous, it appears that in sect. *Anisonema* and groups derived from it evolution has proceeded from a five-carpellate gynoecium by reduction to three, and by multiplication to several carpels. Michaelis (1924: 120) recognized that the gynoecium has undergone both multiplication (e.g., *Hura*) and reduction (e.g., *Antidesma*) in sporophyll number, whereas he found no evidence of multiplication of sporophylls in the androecium.

During the preparation of the present study, a number of difficulties in the terminology of the gynoecium have been encountered; these are mostly due to the conflicting definitions in the literature. Hanf (1934) has proposed a new classification of terms which contains some drastic changes of concept; his system has been explained in translation by Just (1939). According to Hanf's view, each carpel of the angiospermous flower is terminated by a *stylodium*; the term "style" is restricted to apply to the elongated portion of a "coenocarpous" ovary (i.e., one with united carpels). The application of this concept gives the corollary that a single flower can have no more than one style; and in such families as the Ranunculaceae and Caryophyllaceae styles are considered to be absent, flowers of these groups having stylodia only.

Hanf's study of stylar morphology has the great merit of clarifying the relationships between various stylar apparatuses that have become ob-

scured through careless use of terms. However, his definitions are directly contradictory to those current in most systematic works. It seems worth while, therefore, to examine the propriety of adopting such a radically different terminology.

The word "stylodium" was apparently coined by Grisebach in his textbook "Grundriss der systematischen Botanik" (1854). His discussion (in translation) is as follows:

"The boundary between style and stigma is actually established morphologically by the stylar canal, but the designation style and style-arm (rami styli) is applied in systematics to all cylindrical carpel apices, and the [term] stigma is restricted to the glandular part of them. It is therefore appropriate to distinguish the style-like stigmas as stylodes (stylodium) from the true stigmas which are physiologically characterized by their reaction to the pollen grains. According to this definition, for example, the monocarpic pistil of the grasses has one style, two stylodia, and [two] stigmas."

Grisebach (op. cit.) described the gynoeceium of *Euphorbia* as having "stylo tripartito, stylodiis bifidis." In his description of *Cicca antillana* (1857) he still used the term stylodium, but by 1859, in the "Flora of the British West Indian Islands," he had abandoned it. Since the term has not been recently used in systematic literature, the force of custom and usage would appear to weigh against its adoption unless there should be compelling reasons for doing so.

It must be admitted that the word "style" has not always been used with precision. Gray ("Structural Botany," 1879) defined it as the "usually attenuated portion of a pistil or carpel between the ovary and stigma." In the sense of Gray, therefore, the word is a topographical designation and does not imply specific morphological value. The definition given by Fernald (1950): "the usually attenuated portion of the pistil connecting the stigma and ovary" breaks down when applied to a gynoeceium with united carpels but free styles.

Baillon (1858) held a similar concept during his studies on the Euphorbiaceae, for he described the stigma-bearing structures in terms of the style and its branches. Mueller Argoviensis, in his work for the "Prodrromus," at first (1863) described the style of the Euphorbiaceae as " . . . varius, saepius brevius et in tot ramos divisus quot loculi ovarii." But in his generic description of *Phyllanthus* in the finished monograph (1866) he stated: " . . . styli loculis ovariorum isomeri." Mueller thus came to regard the style as the prolongation of the individual carpel rather than of the entire pistil, as he had at first. Pax and Hoffmann (1931) followed the same concept in describing the styles of the Euphorbiaceae as "frei oder verwachsen, wenn frei, dann meist 2-, seltener vielspaltig."

It appears that at least in the Euphorbiaceae the usage of Mueller is perfectly clear and accurate. The style may be defined as the attenuate portion of the carpel (not the pistil) between the ovary and stigma. When the styles are united, as they often are in the Euphorbiaceae, the compound structure may be termed the *stylar column*. The result of this



definition is that the styler column, not the style, of *Phyllanthus* is the morphological equivalent of the style of the Labiatae. Any possible confusion may be obviated, however, by qualifying the latter organ as the "compound style."

The styles of *Phyllanthus* exhibit a remarkable latitude of variation in form, but they may be classified roughly into two types which become distinct at an early stage of development in the bud. In all species investigated the carpel at first is cupuliform with a horseshoe-shaped margin. In one case the adaxial portion of the rim early takes on the form of a "Y" and the carpel apex (i.e., the style) grows out more or less bifid. In the other case the rim retains its original shape longer, and the style is either entire or dilated into an adaxially channelled crenulate or lacerate expansion, the stigma. Since the stigma is not always well-defined, particularly in styles of the first type where the stigmatic surface is discontinuous, the *style-branch* is often the most convenient term.

The great variations in the mature styler apparatus in different species are the result of the interactions of three growth processes: (1) the differentiation of the embryonic carpel apex into "bifid" or "entire" styles; (2) the relative amount of longitudinal vs. transverse growth; and (3) the degree of union between the styles. Many different recombinations of these three processes occur. The styles may be completely united into a column as in *P. ovatus* (sect. *Hemiphyllanthus*) or almost completely free as in sect. *Paraphyllanthus*; the stigmas may be scarcely defined in many species with slender bifid styles, or greatly dilated to form a calyptra as in *P. mirificus*. In species with dilated style-tips, the original adaxial margins of the hippocrepiform embryonic carpel are represented by a pair of adaxial auricles. Usually these are small and sometimes even obsolete, but in some species (e.g., *P. excisus*) they may be quite prominent. In a general way the auricles mark the point at which the styler column ends (when the styles are connate) and the stigmatic surface begins. Below the auricles the stigmatic tissue is usually embedded in the center of the style or styler column and is represented externally only by a slender adaxial suture. Internally, the loose conducting tissue of each style becomes confluent at the point where the tops of the ovarian parts of the three carpels are fused. In most species of *Phyllanthus* a prolongation of this tissue runs into the top of each locule and forms a cap-like structure, the *obturator*, which is closely appressed to the micropylar ends of the ovules (PLATE-FIGS. 48 & 49). Baillon (1858), who first applied the name obturator to this prolongation of the styler tissue, recognized within the present limits of *Phyllanthus* two types of obturators: a single one over both ovules of a locule in *P. salviaefolius* (sect. *Oxalystylis*) and an obturator for each ovule in "*P. grandiflorus*" (identity uncertain). Examination of material in the present study has disclosed in every case a common obturator for both ovules, but its relative development and orientation appear to vary a good deal from species to species. It conspicuously overtops the ovules in *P. subcarnosus* but is nearly vertical in *P. polygonoides* (PLATE-FIG. 49). Unlike *Ricinus*, in which Baillon

reported traces of the obturator in the mature seed, the organ is transient in *Phyllanthus* and atrophies during maturation of the fruit.

The vascular supply of the carpel is quite similar in most of the species of sect. *Phyllanthus* investigated, but needs to be studied in other groups. At the base of the ovary the carpellar bundle divides into one dorsal and two ventral traces. The dorsal trace ramifies into a reticulum on the dorsal surface of the carpel, while the two ventral traces run vertically. The latter first give off the ovular traces and then abruptly bend abaxially and run obliquely across the lateral face of the carpel to join the dorsal reticulum near the base of the styler column. The resulting compound bundle then enters the styler column and bifurcates, each branch forking or remaining unbranched, depending on the character of the style-tips. The point at which the ventral traces leave the axis of the ovary and bend outwards is well-marked by a sharp discontinuity in the tissue, and the upper third of the axis is without vascular supply. The courses taken by the vascular bundles determine to a great extent the configurations of the carpels in the dehiscent fruit. The portion of the axis beneath the "bending-point" of the ventral traces becomes the *columella*, which remains after dehiscence of the fruit as a column projecting from the center of the calyx. The obliquely ascending ventral traces on the lateral faces of the carpels determine the upper line of dehiscence of the cocci, which split on the lateral faces along lines curving away from the ventral traces.

Baillon (1858: 139-140), partly on the basis of his ontogenetic studies, considered the ovules of the Euphorbiaceae to be borne by the axis. From a merely topographic point of view it is correct to say the ovules are "axile," but this need not imply that they are inserted on a structure of "stem" or "branch" nature. The columella, which looks so much like a prolongation of the torus, has no vascular supply independent of the ventral traces, and its extent is exactly determined by the distance these travel vertically before turning outward. The columella is therefore a compound structure derived from the basal parts of the fused ventral margins of the carpels, and is morphologically equivalent to the central placental column of the Caryophyllaceae of the "free-central" placenta of the Primulaceae. There is no evidence to support the assertion of Lam (1948) that the Euphorbiaceae are a "stachyosporous" family (i.e., with sporangia borne on modified branches); the gynoeceum of *Phyllanthus* is not fundamentally different from that of families admitted by Lam to be "phyllosporous."

In *Phyllanthus* each locule of the ovary contains a pair of usually collateral anatropous pendent ovules. The funicle of the ovule is sharply deflected downward from the top of the columellar part of the axis (i.e., about one-third of the way down from the top of the locule), and the hilum is on the side of the ovule toward the center of the ovary. The ovule is more or less barrel-shaped with two integuments, the outer of two cell-layers, the inner of three. The nucellus in all species examined is at least slightly prolonged beyond the exostome of the micropyle as a more or less clavate beak which fills up the space between the micropyle and

the obturator (PLATE-FIG. 49). In species with a relatively massive obturator such as *P. subcarnosus* the nucellar beak, though well-developed, does not project very far beyond the micropyle, but where the obturator is short the tip of the nucellus may be strikingly elongated. In all observed cases there is an intimate contact between obturator and nucellus. The embryo sac, according to Maheshwari and Chowdry (1937), is the normal eight-nucleate type.

Baillon (1858: 613) pointed out that in sect. *Anisonema* the ovules, thought at first collateral, later become obliquely superposed as in *Glochidion*. This change of ovular position is probably due to spatial conditions, since the large number of locules results in a diminished average volume of each one (PLATE-FIG. 47). In all of the three-carpellate gynoecea examined, the ovules are collateral without exception.

### Fruit.

In the great majority of the species of *Phyllanthus* the fruit is a dry thin-walled capsule which often dehisces explosively at maturity. The wall of the fruit is ordinarily composed of two distinct layers which are distinguishable from a rather early stage of the ovary (PLATE-FIGS. 48 & 49). The exocarp, which contains all the vascular supply, is usually thin, scarious, and greenish or reddish at maturity of the fruit; it covers only the outer tangential (abaxial) wall of each coccus. The yellowish endocarp, which lacks vascularization, has a heavily sclerified thick dorsal (tangential) wall and much thinner lateral (radial) walls (PLATE-FIG. 50). When the capsule dehisces, the carpels (now cocci) first separate from one another and from the columella; then the lateral walls split open along an arc as described previously. Often the endocarp also splits vertically along the middle of the dorsal valve, so that the coccus has the form of an irregularly four-valved box loosely enclosing the pair of seeds.

There are a number of species, however, in which the exocarp of the fruit remains fleshy until rather late in ontogeny (e.g., *P. juglandifolius*). In others the exocarp never dries up, and the fruit is either baccate or drupaceous, depending on the degree of sclerification of the endocarp. In *P. reticulatus* (sect. *Anisonema*), which has a baccate fruit, the endocarp is not only tenuous but is not clearly differentiated from the exocarp (PLATE-FIG. 47). In *P. emblica* the ripe fruit is drupe-like with a fleshy exocarp and bony endocarp, but when the fruit eventually dries up the endocarp separates into three massive cocci. The fruit of *P. elsiae* is at first fleshy but on drying the exocarp becomes pithy, while the endocarp is sclerified but thin. In the related *P. acidus* the massive endocarp is bony and indehiscent while the exocarp remains fleshy, so that in this species the fruit is a true drupe with a three- or four-celled putamen. Mueller's description (1886: 413) of the fruit of sect. *Cicca* as capsule-like with two-valved cocci was due to his mistaken inclusion of the very different genus *Margaritaria* in the same section with *Cicca*.

In a general way the type of fruit (i.e., whether dry, baccate, or drupaceous) is definitely related to the habit of particular species. The her-



baceous annual species all have an explosively dehiscent capsule which falls away from a persistent calyx. The shrubby species tend to have a more tardily dehiscent capsule which may fall with the pedicel and columella still attached, and in *P. reticulatus* and *P. subcarnosus* the fruit is fleshy. Finally, in *P. acidus*, *P. elsiae*, and *P. emblica*, all of which are trees, the fruit is drupaceous or "woody." This unmistakable correlation between relative explosiveness of fruit and life-span of plant nicely illustrates adaptation in dispersal capacity which must have a basis in natural selection. It also indicates that fleshiness of fruit *per se* may not always be a reliable mark of affinity, and is consequently of little value as a generic character.

### Seed.

Usually there is a pair of seeds in each cell of the fruit of *Phyllanthus*, each of which has a trigonous outline due to compression against one another and the locule walls. Sometimes, however, only one of the seeds will attain full size, and the other will be under-developed. In sect. *Cicca* the relative development of the pair of seeds is most variable, for there may be either two equal seeds, one large and one small, or one large one only; and locules in which these three types occur may be found in a single fruit. In *P. emblica* the seeds of a pair are unequal, but both appear viable. Swartz (1800) characterized the seeds in the fruits of the West Indian sect. *Epistylum* as "subsolitaria"; this may be correct, but in the other native West Indian species there are nearly always two equal seeds in each locule. The tendency towards abortion of one of the ovules, which is also noticeable in the genus *Savia*, indicates the existence of a reduction trend toward the uniovulate condition of the Crotonoideae. However, in all of the Phyllanthaceae so far investigated the suppression of the second ovule takes place late in ontogeny, probably after anthesis; even though a locule of the mature fruit may have only one seed, examination of the ovary at an early stage has always shown two ovules in each cell.

The development of the seed-coat from the integuments appears to be somewhat variable and requires further investigation. The epidermal layer of the outer integument usually becomes variously modified during maturation of the seed; the resulting diversity in ornamentation of the testa provides convenient taxonomic characters for recognizing or distinguishing many species. Only rarely is the seed-coat quite smooth and uniformly colored as it is in *P. hyssopifolius* (PLATE-FIG. 57). In *P. juglandifolius* the seed-coat, although smooth, has a mottled appearance somewhat like that of *Ricinus* (PLATE-FIG. 64). Many different species have the seed-coat covered with raised dots, or points, which may be regularly or irregularly arranged; seeds of this type may be termed verruculose (PLATE-FIGS. 51, 52, 59). A great number of other species have seeds which though nearly smooth are seen under a lens to be covered with fine lines or ridges, on close inspection. Often the epidermal cells, which usually have their long axes transverse to the long axis of the seed, are so translucent that the cells of the subepidermal layer (which run

parallel to the long axis) show through. This gives the effect of longitudinal striae crossed by very fine striolae (PLATE-FIG. 55). In some of the herbaceous species of sect. *Phyllanthus* the seed-coat is very highly specialized. When the seeds of *P. junceus*, *P. echinospermus*, or related species, are placed in water they change from finely ridged or striate to "hispid" in appearance. Microscopic examination shows that this reaction is due to peculiar hygroscopic epidermal cells which are heteropolar: one end has conspicuously uneven wall-thickenings which give the lumen a scalloped outline, while the other is smoothly and less massively thickened. Slightly excentric toward the "smooth" end is a median peg of cellulose which runs through the lumen between the tangential walls. When the seed is wetted the longer unevenly thickened cell-ends swell out on the adaxial side and assume the form of concave arcs, while the shorter ends remain appressed to the surface of the seed; the projecting ends thus give the appearance of trichomes projecting from the seed-coat. This behavior presumably allows greater penetration of water into the seed-coat and consequently earlier germination of the seed. Such an adaptation, combined with the explosively dehiscent capsule, affords these herbaceous species a highly efficient mechanism for rapid dispersal and ecesis.

The seed of *P. urinaria* has a curious and unique kind of seed ornamentation (PLATE-FIGS. 53 and 54). The seed-coat is not only provided with sharp transverse ridges, but it has in addition deep pits on the sides; this combination of characters makes the seeds of *P. urinaria* unmistakable among those of the West Indian species. The deep pits on the radial walls perhaps represent a different sort of adaptation for permitting rapid penetration of water and faster germination.

In *P. orbicularis* developmental study has clearly shown that the heavily sclerified "palisade" layer of the seed-coat is developed from the outer layer of the inner integument (PLATE-FIG. 50); it is this layer which imparts to the seed most of its mechanical strength. In *P. orbicularis*, the middle layer of the inner integument is very inconspicuous in the seed, but the inner layer, though not enlarged, stands out because the cells are all filled with tannin. It will be noted that in this species, the two layers of the outer integument are relatively unimportant and not noticeably specialized. Too few species have been studied to know if the ontogeny of the seed is similar in every species; it is possible that in some species the sclerified layer is derived from the inner layer of the outer integument, but this remains to be demonstrated.

The mature embryo, which is embedded in rather copious whitish cartilaginous endosperm, ordinarily has a slender terete radicle and broad foliaceous cotyledons (e.g., in *P. juglandifolius*). In some of the herbaceous species (e.g., *P. amarus*), however, the cotyledons are narrowly oblong and only slightly broader than the radicle. Sometimes the embryo is slightly curved; Gaertner (1791: 125, pl. 108) described and illustrated the seed of *P. maderaspatensis* as having a "subspiral" embryo. Gaertner (op. cit. 127, pl. 109) clearly distinguished *Glochidion* on the basis of its very distinctive seeds, in which the seed-coat is fleshy and the hilar cavity

so enormously enlarged that the embryo is deformed; unfortunately, he chose to describe the genus under Banks' manuscript name *Bradleja*. This seed character, so clearly pointed out by Gaertner, is one of the best features for distinguishing *Glochidion*. Unfortunately, it has been passed over in recent years, with the result that the boundary between *Glochidion* and *Phyllanthus* has appeared weaker than it actually is.

#### CYTOLOGY

The cytology of *Phyllanthus* remains one of the poorest known areas of the morphology of the genus. Perry (1943), in the only previous specific contribution to the cytology of the Phyllanthaceae, found a diploid number of 28 in *P. carolinensis* and *P. emblica*; he suggested that the basic number is 7 and that these species are therefore tetraploids. On the basis of his finding a diploid number of 56 in *Breynia*, he concluded that the latter is closer to *Phyllanthus* than one would judge from the treatment of Pax and Hoffmann (1931); evidence from other fields tends to support his statement. On the other hand Perry observed a diploid number of 16 in *Securinega obovata* [= *Flueggea virosa*]. This apparent difference in base-number indicates that further investigations in the Phyllanthaceae should produce interesting data for purposes of determining evolutionary relationships.

The only additional species whose chromosome number has been investigated is *P. juglandifolius* (sect. *Asterandra*), root-tip preparations of which were made by Dr. E. G. Voss from material in the University of Michigan Botanical Gardens. The diploid number as seen in root-tip smears of this species is approximately 160; the number is so large that both of us could agree only that it lies between  $20n$  and  $24n$  (assuming 7 as the basic number), and is probably closer to 168 than to 140. Although one can scarcely draw any far-reaching conclusions on the basis of the chromosome complement in only three species out of 650, the very high chromosome number in *P. juglandifolius* is quite suggestive. It indicates that amphidiploidy might have occurred repeatedly during the evolution of the West Indian species related to sect. *Asterandra*, and raises the possibility that the difficulty in determining relationships within the genus may be due to ancient hybridizations between rather widely separated species. Cytological examination of additional species from tropical America can hardly fail to throw considerable light on the difficult problem of intrageneric relationships. Unfortunately all efforts to germinate seeds of the shrubby species of sects. *Elutanthos*, *Williamia*, *Orbicularia*, and *Thamnocharis* have been unsuccessful. Collection of cytological specimens in the field may be the only means of successfully attacking the problem.

Perry has concluded from his data that "it appears that the direction of evolution in this family has been from the annual to the perennial condition, as was found for the Crassulaceae, Leguminosae, Ranunculaceae." Apparently he was impressed by the fact that some of the herbaceous species have lower chromosome numbers than the woody ones. However,



on the basis of morphological evidence other than chromosomes there is no doubt that at least in *Phyllanthus* the annuals are definitely derived from shrubby or suffruticose ancestors; and this is surely true of the Euphorbiaceae as a whole. The higher chromosome number of woody species is itself not a reliable indicator of primitiveness; Stebbins (1950) and others have shown that the arboreal habit tends to favor polyploidy during the course of evolution.

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(To be continued)

## EXPLANATION OF PLATES \*

### PLATE I. GROWTH FORM.

FIG. 1. *Phyllanthus platylepis* Small (grown from seed of Webster 3651, Levy Co., Fla.).

FIG. 2. *Phyllanthus pachystylus* Urb. (Webster 3906, Moa region, Cuba), 1/10 natural size.

FIG. 3. *Phyllanthus tenellus* Roxb. (cult. Univ. of Michigan Bot. Gardens), 1/4 natural size.

FIG. 4. *Phyllanthus juglandifolius* Willd. (cult. Univ. of Michigan Bot. Gardens).

### PLATE II. BRANCHLET ANATOMY. (× 50)

FIG. 5. *Phyllanthus reticulatus* Poir. (Webster 5237, Jamaica); cross-section of branchlet slightly above the node. At the bottom of the picture is the petiole and the two stipules. FIG. 6. Section through nodal region, showing trilacunar node with lateral stipular traces.

FIG. 7. *Phyllanthus maleolens* Urb. & Ekm. (Holdridge 1381, Haiti [MICH]); cross-section of branchlet through nodal region, showing trilacunar node with large stipular traces.

\* Voucher specimens are deposited at both the University of Michigan and Harvard University herbaria, except where another herbarium is specifically indicated.

FIG. 8. *Phyllanthus williamoides* Griseb. (Webster 4014, Cuba); cross-section of branchlet.

### PLATE III. STEM ANATOMY. ( $\times 50$ )

FIG. 9. *Phyllanthus botryanthus* Muell. Arg. (Harvard slide 2922, probably from Curran & Haman 164, Curaçao); cross-section of mature stem. FIG. 10. Tangential section.

FIG. 11. *Phyllanthus emblica* L. (Harvard slide 2120, Cuba); tangential section. FIG. 12. Radial section.

FIG. 13. *Phyllanthus pachystylus* Urb. (Webster 3906, Cuba); vessel elements.

### PLATE IV. PHYLLOCLADES.

FIG. 14. *Phyllanthus*  $\times$  *elongatus* (Jacq.) Steud. (Webster s.n., cult. Harvard greenhouse); cross-section of penultimate axis,  $\times 25$ . FIG. 15. Cross-section of ultimate axis,  $\times 40$ . Both axes are still so young that the sclereids in the cortex are not yet hardened.

FIG. 16. *Phyllanthus epiphyllanthus* L. (Jervis 1368, Cuba); cross-section of phylloclade, taken from dried specimen,  $\times 72$ . The dark brown masses represent the compacted remains of the tannin-filled cortical parenchyma cells. Note the concentric bundles.

FIG. 17. *Phyllanthus montanus* Sw. (Webster 5637, Jamaica); cross-section near tip of phylloclade,  $\times 72$ . The structure on the right is a scale-leaf. Note that at this level palisade tissue is developed only on one side.

### PLATE V. STOMATA ( $\times 175$ )

FIG. 18. *Phyllanthus microdictyus* Urb. (Webster 3809, Cuba); in this, and the following figures, the upper epidermis is shown on the left-hand side of the figure and the lower epidermis on the right-hand side.

FIG. 19. *Phyllanthus heliotropus* Wright ex Griseb. (Shafer 10708, Cuba [US]).

FIG. 20. *Phyllanthus selbyi* Br. & Wils. (Britton et al. 14157, Isle of Pines).

FIG. 21. *Phyllanthus niruri* L. (Britton et al. 6438, Puerto Rico [NY]).

### PLATE VI. LEAF ANATOMY.

FIG. 22. *Phyllanthus scopulorum* (Britton) Urb. (Webster 3849, Cuba); cross-section of nearly mature leaf, from specimen preserved in FAA,  $\times 40$ .

FIG. 23. *Phyllanthus ekmanii* Webster (Jervis 3650, Cuba); cross-section of mature leaf, from dried specimen,  $\times 35$ .

FIG. 24. *Phyllanthus microdictyus* Urb. (Webster 3809, Cuba); cleared leaf-blade,  $\times 85$ .

FIG. 25. *Phyllanthus incrustatus* Urb. (Shafer 4453, Cuba [NY]); cleared leaf at focus just beneath upper epidermis, showing arrangement of sclereids,  $\times 85$ .

FIG. 26. *Phyllanthus comosus* Urb. (Webster 3883, Cuba); marginal area of cleared leaf,  $\times 85$ .

FIG. 27. *Phyllanthus formosus* Urb. (Shafer 4102, Cuba [NY]); marginal area of cleared leaf,  $\times 85$ .



PLATE VII. LEAF VENATION. ( $\times 50$ ).

FIG. 28. *Phyllanthus emblica* L. (Jack 4246, Cuba).

FIG. 29. *Phyllanthus botryanthus* Muell. Arg. (Triana 3664, Colombia).

FIG. 30. *Phyllanthus reticulatus* Poir. (Britton 4067, Jamaica [NY]).

FIG. 31. *Phyllanthus chryseus* Howard (Webster 3853, Cuba).

FIG. 32. *Phyllanthus scopulorum* (Britton) Urb. (Webster 3849, Cuba).

FIG. 33. *Phyllanthus spathulifolius* Griseb. (Webster 3896, Cuba).

## PLATE VIII. POLLEN GRAINS.\*

FIG. 34. *Phyllanthus niruri* L. (Ekman H16515, Hispaniola [S]).

FIG. 35. *Phyllanthus trigonus* Urb. (Ekman H2792, Hispaniola [S]); polar view, outer focus.

FIG. 36. *Phyllanthus acuminatus* Vahl (Wright 1938, Cuba [S]); more or less equatorial view, outer focus.

FIG. 37. *Phyllanthus heliotropus* Wr. ex Griseb. (Ekman 10735, Cuba [S]).

FIG. 38. *Phyllanthus vaciniifolius* (Muell. Arg.) Muell. Arg. (Sandwith 1315, Br. Guiana [S]).

## PLATE IX. POLLEN GRAINS.

FIG. 39. *Phyllanthus carnosulus* Muell. Arg. (Wright "714", Cuba [GOET]).

FIG. 40. *Phyllanthus berterioanus* Muell. Arg. (Leonard 8826, Hispaniola [NY]); upper right-hand quadrant shows the appearance at outer focus.

FIG. 41. *Phyllanthus subcarnosus* Wr. ex Muell. Arg. (Wright 1946, Cuba [S]); insert shows the appearance of the grooves at outer focus (i.e., very narrow).

FIG. 42. *Phyllanthus maleolens* Urb. & Ekm. (Ekman H6849, Hispaniola [S]).

FIG. 43. *Phyllanthus distichus* Hook. & Arn. (Degener 11645, Hawaiian Islands).

FIG. 44. *Phyllanthus pulcher* Wall. ex Muell. Arg. (Broadway 5459, Trinidad [S]).

## PLATE X. FLORAL ANATOMY.

FIG. 45. *Phyllanthus chryseus* Howard (Webster 3853, Cuba); longitudinal section of male flower bud,  $\times 30$ .

FIG. 46. *Phyllanthus reticulatus* Poir. (Webster 5237, Jamaica); longitudinal section of male flower, showing stomatal pits in disk,  $\times 30$ . FIG. 47. Cross-section of female flower,  $\times 30$ .

FIG. 48. *Phyllanthus*  $\times$  *elongatus* (Jacq.) Steud. (Webster s.n., cult. Univ. of Michigan greenhouse); cross-section of ovary at the level of the obturators,  $\times 45$ .

FIG. 49. *Phyllanthus polygonoides* Nutt. ex Spr. (Webster & Wilbur 2965, Texas); longitudinal section of ovary showing association of obturator and nucellar beak,  $\times 100$ .

\* The drawings in plates VIII and IX are semi-diagrammatic and (except for figs. 35, 36, and 40) indicate the appearance of the exine at roughly the level of the base of the individual sculptural elements (muri or pilae). All drawings are on the scale of 1 cm. = 5.9  $\mu$ .

FIG. 50. *Phyllanthus orbicularis* HBK. (Webster 3867, Cuba); longitudinal section of immature fruit,  $\times 100$ . Above, ovary wall; in the center, two seeds showing the two cell-layers of the outer integument and the three of the inner.

## PLATE XI. SEEDS.

FIG. 51. *Phyllanthus pudens* L. C. Wheeler (Bush 906, Texas [GH]); verruculose ornamentation,  $\times 22$ .

FIG. 52. Ventral and radial view,  $\times 7$ .

FIG. 53. *Phyllanthus urinaria* L. (Cory 49975, Texas [GH]); transversely barred ornamentation,  $\times 45$ .

FIG. 54. Ventral and radial view,  $\times 14$ .

FIG. 55. *Phyllanthus amarus* Schum. & Thon. (Small & Small 6818, Florida [GH]); finely (longitudinally) ribbed ornamentation,  $\times 45$ .

FIG. 56. Ventral and radial view,  $\times 14$ .

## PLATE XII. SEEDS.

FIG. 57. *Phyllanthus hyssopifolius* HBK. (Ekman H15612, Hispaniola [S]),  $\times 12$ .

FIG. 58. *Phyllanthus emblica* L. (Jack 4246, Cuba [NY]),  $\times 6$ .

FIG. 59. *Phyllanthus niruri* L. (Parks 14595, Texas [GH]),  $\times 12$ .

FIG. 60. *Phyllanthus williamoides* Griseb. (Webster 4014, Cuba),  $\times 6$ .

FIG. 61. *Phyllanthus pachystylus* Urb. (Webster 3906, Cuba); mature carpel, or coccus, showing two seeds in position,  $\times 6$ . Note the crescent-shaped split in the radial walls of the carpel, and the separation of the two layers of the tangential wall. FIG. 62. Seeds,  $\times 6$ .

FIG. 63. *Phyllanthus nutans* Sw. (Britton 929, Jamaica [NY]),  $\times 6$ .

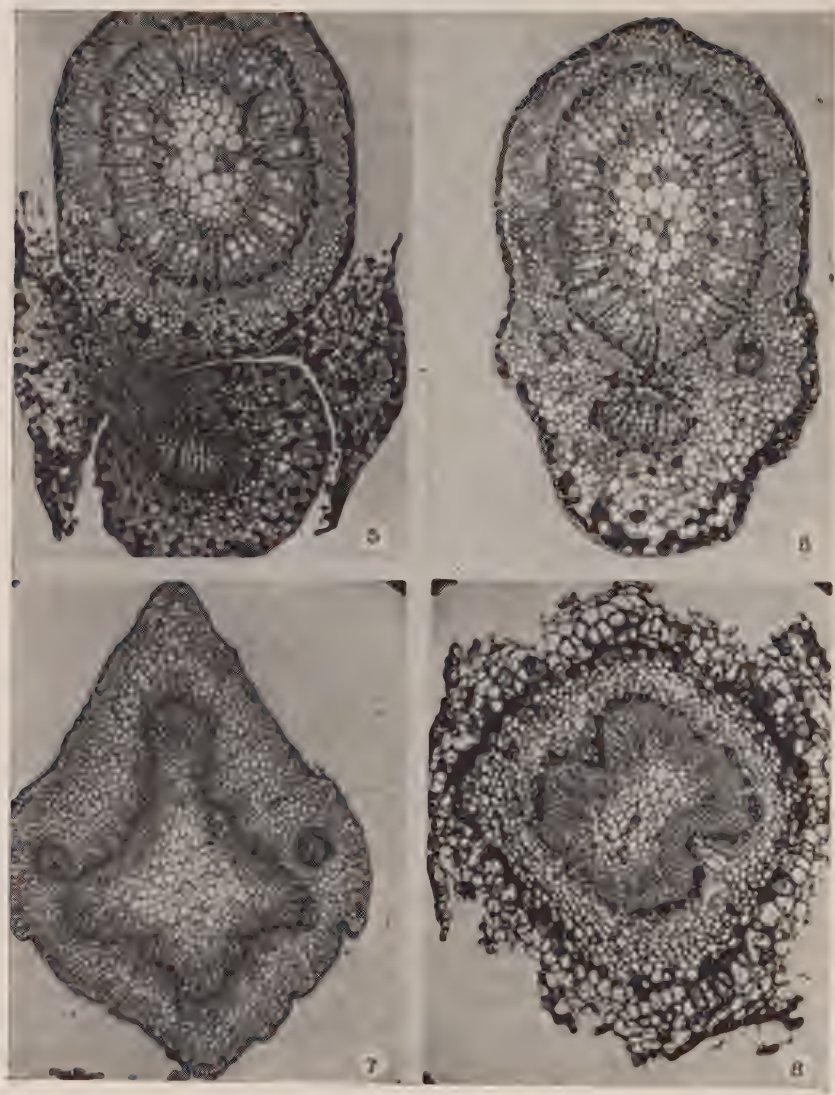
FIG. 64. *Phyllanthus juglandifolius* Willd. (Webster 4028, Cuba),  $\times 6$ .

FIG. 65. *Phyllanthus ekmanii* Webster (Ekman 6206, Cuba [S]),  $\times 6$ .

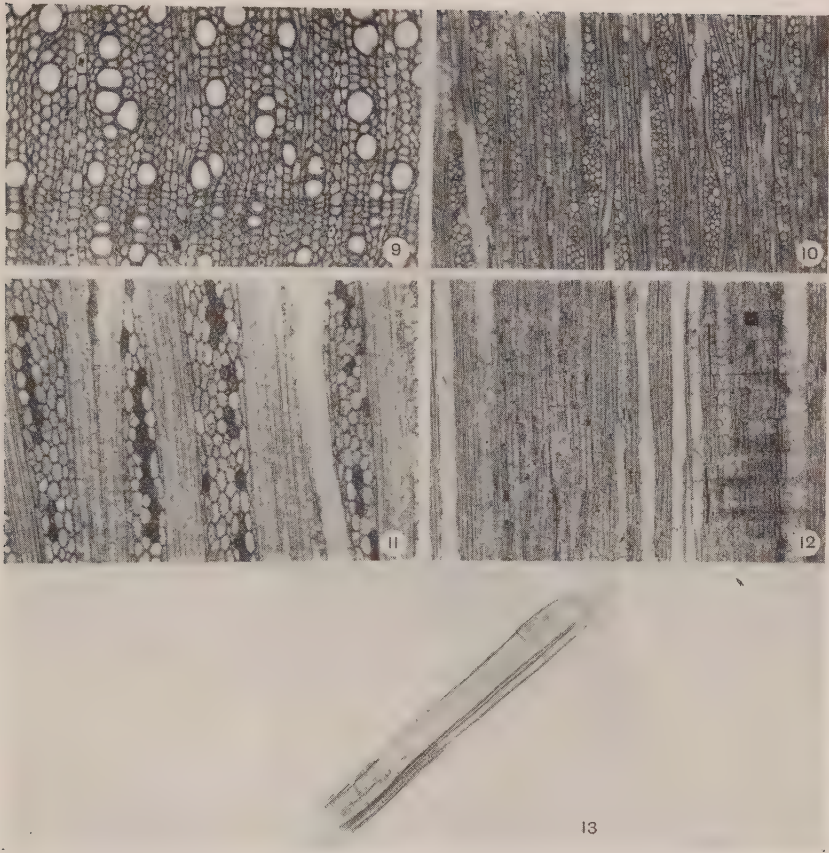


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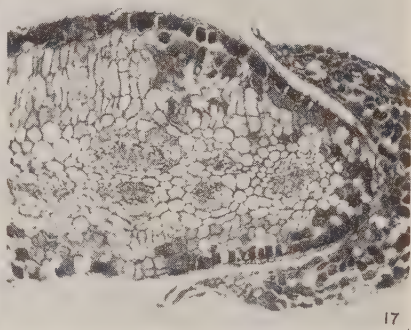
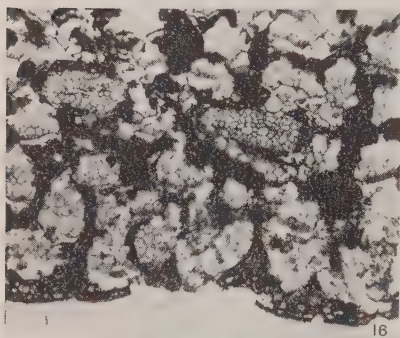
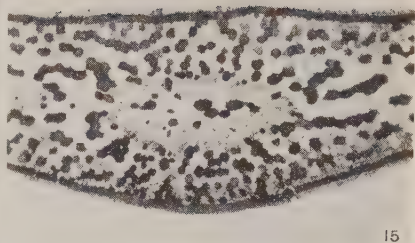




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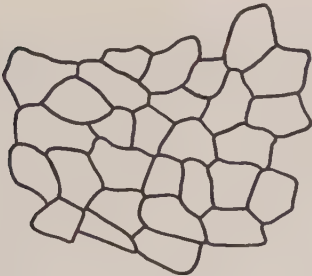


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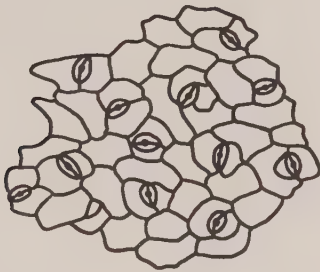
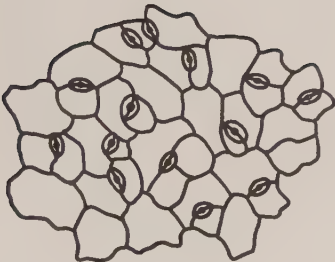


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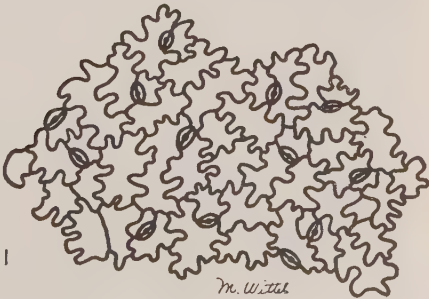
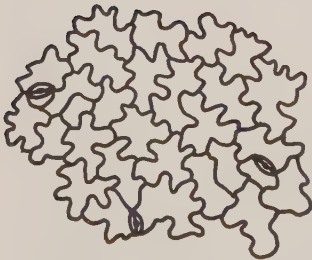
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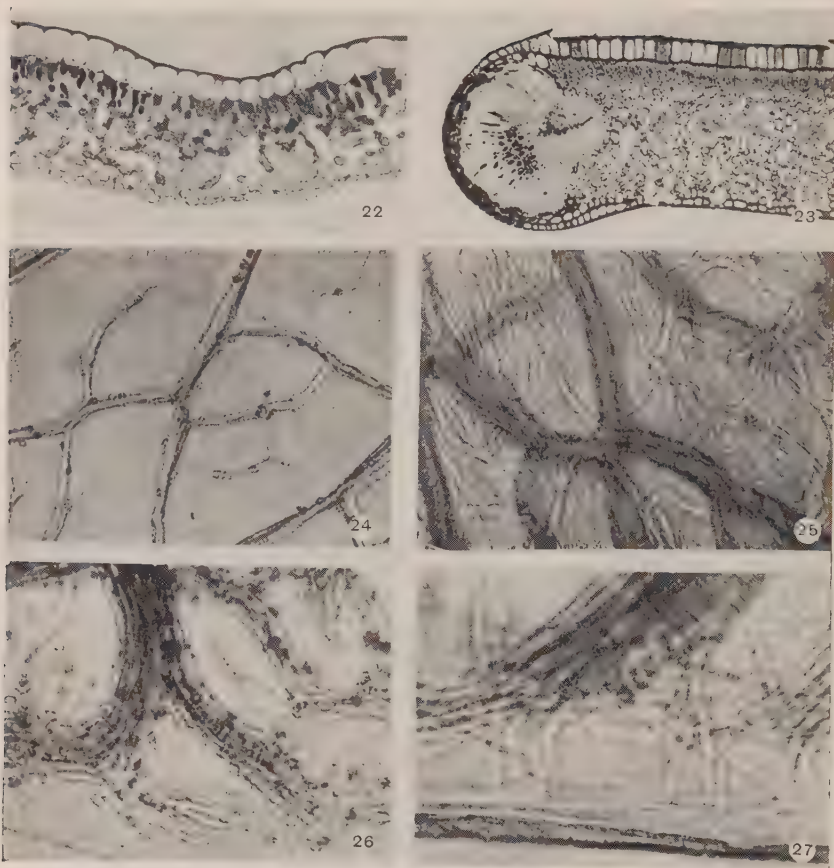


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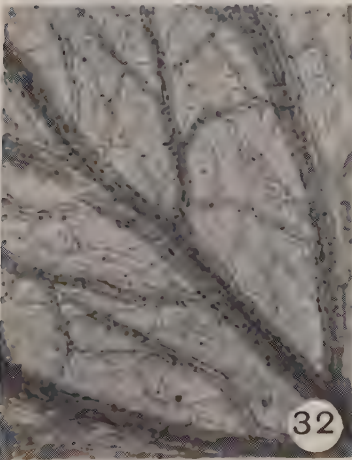
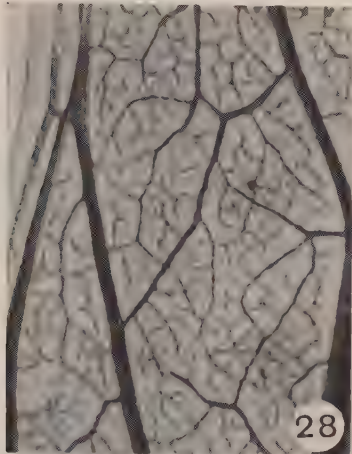


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*M. W. Will*

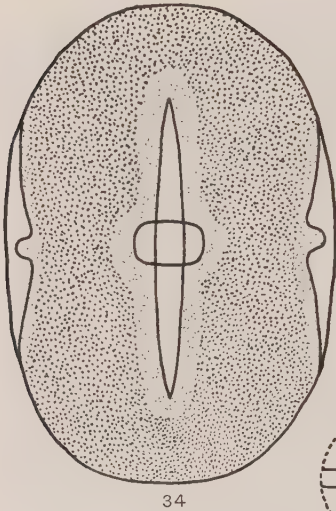


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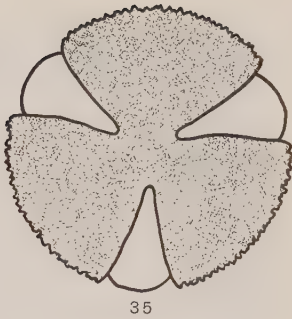


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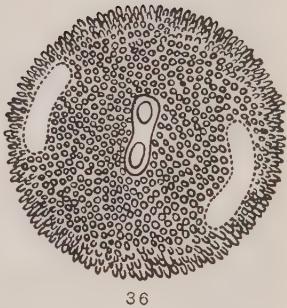




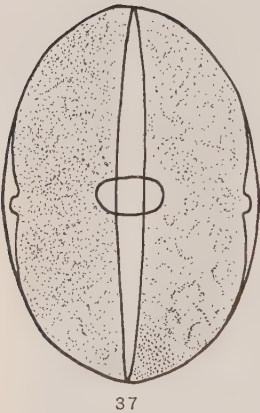
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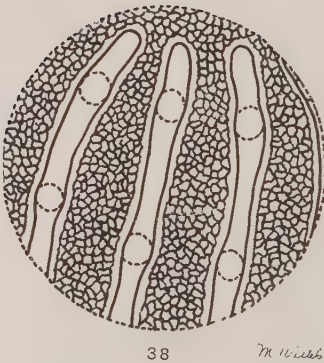
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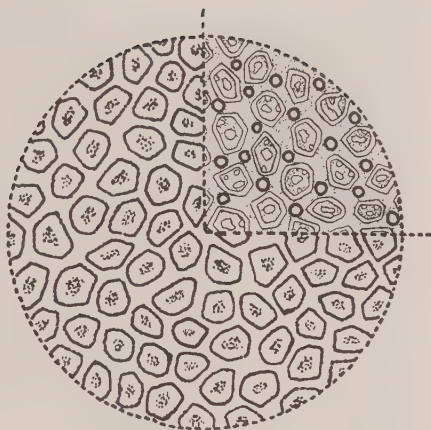
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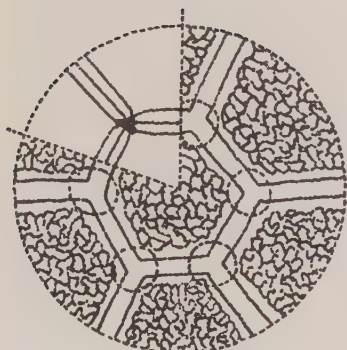
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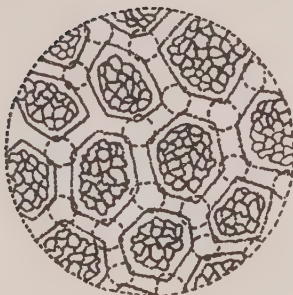
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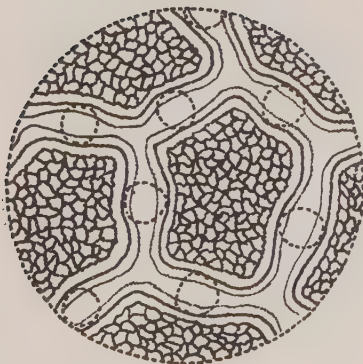
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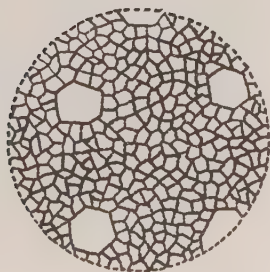
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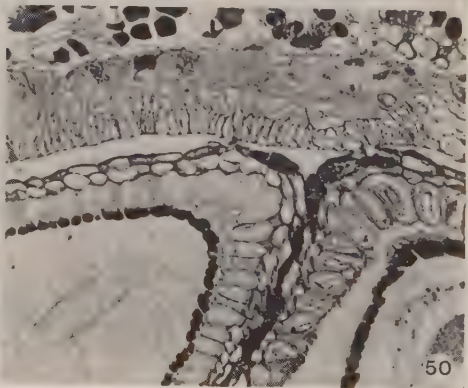
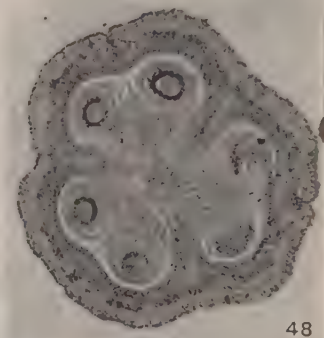
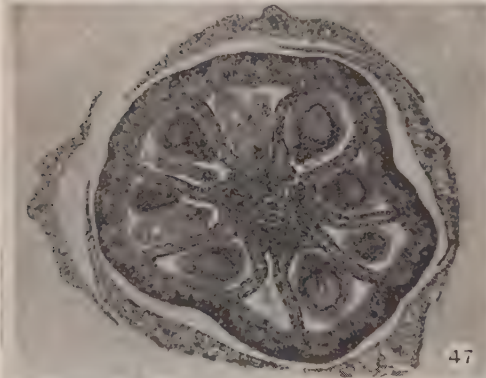
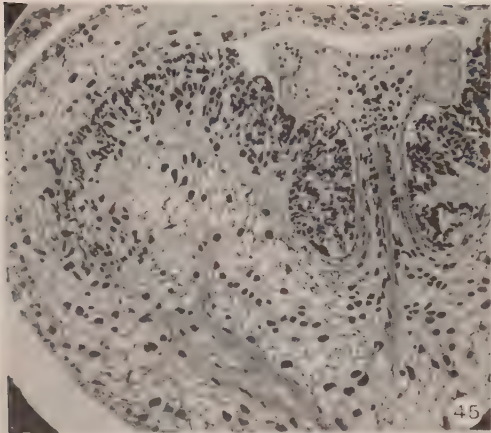
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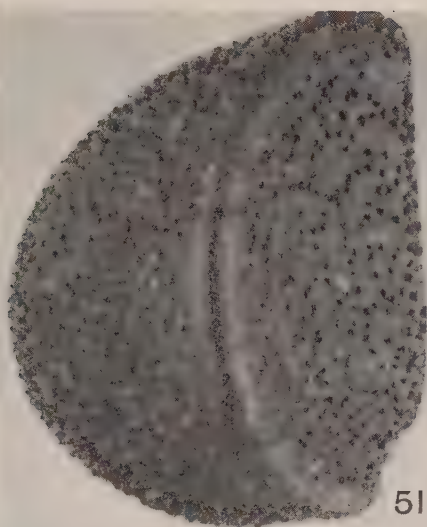


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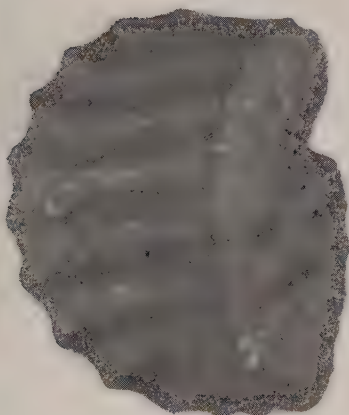




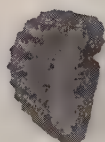
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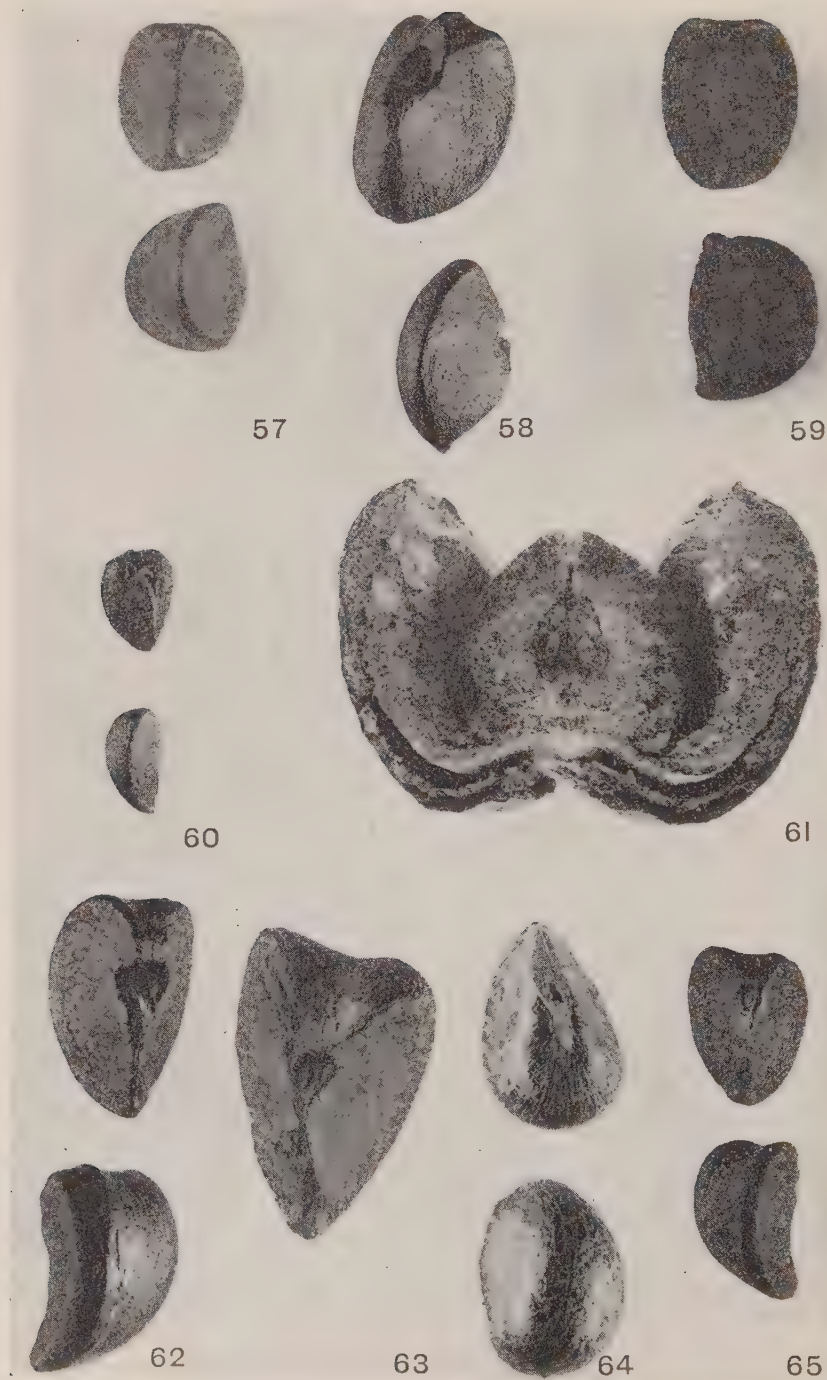
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WEBSTER, WEST INDIAN PHYLLANTHUS

## NODAL ANATOMY IN RETROSPECT

I. W. BAILEY

## INTRODUCTION

IN 1913, Professor E. W. Sinnott and I initiated a series of cooperative investigations on the phylogeny of the angiosperms which led us to the publication of nine papers between 1914 and 1918. Summations of evidence accumulated during the last forty years have supported and strengthened our contention (20) that ancestral angiosperms were relatively large woody perennials, and that the herbaceous habit in dicotyledons is a derived, rather than a primitive one. Similarly, much additional information has verified our conclusion (1) that the structure of the xylem in such representatives of the Amentiferae as the Casuarinaceae, Betulaceae and Fagaceae is relatively highly specialized rather than truly primitive. On the contrary, our conclusions regarding the ancestral form and vasculature of the angiospermic leaf need reconsideration in the light of investigations of a wider range of material.

## GENERALIZATIONS REGARDING NODAL ANATOMY

As a result of an extensive reconnaissance of 34 orders and 164 families of dicotyledons, Sinnott (18) emphasized the fact that there are three significant forms of foliar nodal anatomy in angiosperms, viz., the *unilacunar* form, in which the vascular supply of the leaf is related to a single gap in the stele, the *trilacunar* form, in which the vascular strands are related to three distinct and more or less widely separated gaps, and the *multilacunar* form, in which numerous lateral vascular strands are related to independent gaps. Although a number of dicotyledonous families are pre-vaillingly unilacunar, trilacunar or multilacunar — thus providing significant evidence in the identification and classification of plants — there are a considerable number of families and numerous orders in which transitions between the different forms of nodal anatomy occur. Sinnott concluded that the trilacunar condition is primitive in angiosperms, the multilacunar form having arisen by amplification of the number of independently attached lateral strands, and the unilacunar form (a) in certain families, by the reduction and elimination of the two lateral strands and (b) in other families, by the approximation of the median and lateral strands forming an aggregation of three strands that is related to a single gap in the stele.

These conclusions, in which I concurred, were based upon putative phylogenetic evidence derived from the angiosperms as a whole, and upon ontogenetic sequences that occur in the developments of specific plants. The trilacunar condition tends to predominate in a majority of the families of the



Archichlamydeae, the unilacunar structure in the Centrospermae, Myrtiflorae and a majority of the families of the Metachlamydeae. The multilacunar condition is characteristic of many of the Polygonaceae, Platanaceae, Simarubaceae, Burseraceae, Meliaceae, Araliaceae and Umbelliferae. Transitions to unilacunar structures frequently occur in trilacunar families in representatives which exhibit an enhanced degree of both floral and anatomical specialization. Similarly, aberrant transitions to multilacunar nodal anatomy occur in many predominantly trilacunar orders and families. Where the leaves of adult plants are multilacunar, the first-formed leaves of seedlings commonly are trilacunar with transitions to the typical multilacunar condition in successively formed ones. Similarly, the first leaves of monocotyledonous seedlings frequently have three independently attached vascular strands, thus resembling the trilacunar-like structure that occurs in the adult leaves of putatively more primitive representatives of the Potamogetonaceae.

#### STATISTICAL CORRELATIONS REGARDING LEAF FORM

In a subsequent comprehensive survey of 156 families of dicotyledons, we (19) demonstrated that there is an evident correlation between nodal anatomy and the formation of stipules. Of 75 of these families, which have stipules or leaf sheaths, 53 are characterized by having trilacunar or multilacunar nodal structure, and in five others this form of nodal anatomy is common. In 16 of these stipulate families the nodes are unilacunar, but in 11 of them the stipules frequently are poorly developed, minute or absent. Conversely, of 81 exstipulate families 52 are characteristically unilacunar and two more are frequently so. Where unilacunar structure occurs in aberrant genera or species of dominantly stipulate and trilacunar families, such plants commonly exhibit reduction or elimination of stipules. Conversely, aberrant trilacunar representatives of dominantly unilacunar families not infrequently have well-developed stipules in contrast to their unilacunar relatives. Among exstipulate trilacunar families approximately 75% of the plants have leaves or leaflets with entire margins. Thus, the fullest development of stipules occurs in trilacunar families having lobed leaves or leaves with dentate, serrate or glandular margins, whereas the strongest tendency toward the reduction and elimination of stipules occurs in unilacunar families having leaves with entire margins. It is significant in these connections that the vasculature of most stipules is related to the lateral vascular strands at some level of the node or petiole.

As a result of extensive statistical analyses of dicotyledonous floras in diversified phytogeographical regions of the principal continental areas, we (21) concluded that the primitive angiospermic leaf was simple, palmately veined, probably 3-lobed, and was provided with three main vascular strands which were attached at a trilacunar node. These conclusions were based upon evidence from *paleobotany*, that the palmate leaf was more frequent in the Cretaceous and Tertiary than at present; from *comparative morphology*, (a) that there is a correlation between the palmate leaf and

trilacunar (and multilacunar) nodes, (b) that there is a strong correlation between the simple pinnate leaf and the unilacunar node, (c) that palmate or parallel venation tends to predominate in cotyledons and floral appendages; and from *phylogeny*, that palmate leaves are more frequent in relatively primitive groups of dicotyledons and that pinnate leaves are commoner in more advanced ones. Furthermore, among woody plants the trilacunar (more ancient) nodal condition predominates in temperate regions, and the unilacunar (more advanced) in the tropics. The palmately lobed leaf among woody plants is largely confined to temperate regions. These facts, in company with others, suggested that the dicotyledons first appeared under a climate more temperate than tropical, a climate in the Mesozoic presumably found extensively only in the uplands.

### REVIEW OF PHYLOGENETIC EVIDENCE

The most comprehensive and reliable phylogenetic sequence thus far revealed among the higher plants is the derivation of vessels from scalariformly pitted tracheids in the angiosperms. As demonstrated by large volumes of data successively accumulated during the last 40 years, the complete evolutionary story is preserved among living angiosperms, and it is no longer essential to search geological strata for "missing links." Furthermore, this particular phylogenetic sequence clearly is a unidirectional and irreversible one, and cannot be read in reverse, as so frequently happens, since in view of available information regarding the structure of the lower vascular land plants tracheids cannot logically be derived from the dissociated members of vessels.

It should be emphasized in this connection that the evolution and specialization of vessels in angiosperms have been reconstructed *entirely independently* of assumptions regarding the relative 'primitiveness' of specific orders, families or other taxa of the angiosperms. Although primitive vesselless forms of dicotyledonous xylem are confined at present to woody plants of putative ranalian affinities, viz., Winteraceae, *Trochodendron*, *Tetracentron*, *Amborella* and *Sarcandra*, relatively primitive stages in the evolution of vessels are preserved in such families of the Metachlamydeae as the Clethraceae, Ericaceae, Symplocaceae, Styracaceae and Caprifoliaceae, as well as in various families of the Archichlamydeae. Conversely, highly evolved and specialized vessels occur in many representatives of such putatively primitive taxa of the Archichlamydeae as the Amentiferae, Ranales, Rosales, Malvales, etc. Thus, it is now clearly demonstrated that evolutionary modification of the xylem of stems and roots is *not necessarily* closely synchronized with phylogenetic trends in the specialization of the angiospermic flower. Either trend of evolution may be accelerated or retarded in relation to the other. For example, among primitively vesselless genera of the dicotyledons, certain of them, e.g., *Zygogynum*, *Trochodendron*, *Sarcandra*, exhibit advanced stages of floral specialization. Therefore, although one of the various classifications of the angiosperms may possibly provide a fairly accurate picture of certain

aspects of floral evolution, it evidently does not afford a truly phylogenetic classification of the plants which bear the flowers, i.e., when evidence from all organs and parts of the plants is taken into consideration. Nor can a truly natural classification of plants as a whole be attained by substituting phylogenetic trends, however reliable, from another *single* organ or part of the plant.

In view of such facts as these, there obviously are inherent difficulties and dangers in attempting to determine the primitive form and vasculature of the angiospermic leaf by statistical analyses of the various families and orders of the Archichlamydeae as contrasted with the Metachlamydeae, or in basing conclusions upon speculative assumptions that have been made regarding the relative primitiveness of the Amentiferae, Ranales, Rosales, Malvales, etc.

In the case of the vessel, paleobotanical evidence demonstrates that it can be derived only by modification of *one* type of cell, viz., tracheid. On the contrary, in the case of the angiospermic leaf, the possibility exists that it may have been derived from one of *several* diversified forms of potentially ancestral foliar appendages. Furthermore, the possibility exists that changes in form and vasculature may at times be reversible. In other words, in the case of the vessel convincing evidence is now available regarding initial stages of a unidirectional and irreversible evolutionary trend, whereas in the case of the leaf no comparably reliable information is available as yet.

#### REVIEW OF NODAL ANATOMY

Sinnott's and my conclusions regarding the primitive form of the angiospermic leaf were based largely upon our contention that in angiosperms unilacunar and multilacunar nodal structures are derived from a primitive trilacunar one. Since a similar working hypothesis was subsequently adopted by Eames (6) in the study of floral appendages, it is evident that nodal anatomy became the keystone in a large volume of phylogenetic investigation. Thus, it is essential to determine how reliable a working hypothesis is provided by nodal anatomy.

Among ferns, seed ferns, Cordaitales, Bennettitales (*sensu lato*), Coniferales, *Ginkgo* and *Ephedra*, the vascular strands of the leaf, whether one, two or many, are related to a single gap in the primary body. Deviations from this prevailing *unilacunar* condition occur, however, in the living cycads and in *Gnetum*, where numerous foliar strands are related to an equivalent number of independent gaps in the stele. Such evidence from the lower Pteropsida suggests that a unilacunar type of node is primitive, and that the multilacunar condition among gymnosperms is a derived and specialized one. Therefore, the trilacunar and multilacunar structures of angiosperms must have been derived at some evolutionary stage from a unilacunar condition. Whether the transition occurred within the angiosperms themselves or during the evolution of their ancestors is a basic problem in need of solution. Are all forms of unilacunar nodes homologous or are there



fundamental structural differences that have been overlooked? If the early angiosperms acquired a pair of independently attached foliar strands and subsequently eliminated them by reduction or approximation, does the resulting unilacunar condition differ structurally from the primitive nodal anatomy of the lower Pteropsida?

Much of the work in the past has dealt with comparative investigations of fully matured structures at nodal levels. Such comparative studies of end products have proven to be of significant value in the identification and classification of plants, but, without comprehensive developmental investigations at successive levels of the shoot and leaf, they may be misleading at times in the study of phylogeny.

There has been an increasing tendency of late to visualize the vasculature of the stem and its appendages in terms of the "Telome Theory." Thus, particularly in the case of the Cordaitales and Coniferales, the leaf trace is illustrated as a single strand which may dichotomize one or more times in its upward extension into the leaf. In such plants there may be two separate vascular strands (related to a single gap) at the nodal level, with more or less numerous additional dichotomies occurring within the lamina of the leaf. It is significant in this connection, however, that in *Ginkgo biloba* L. as demonstrated by Gunckel and Wetmore (11, 12), in certain species of *Ephedra* (14, 15), and in such dicotyledons as *Austrobaileya* (3, 14), *Trimenia* (14, 16), *Ascarina* (22), *Lactoris* (23), and *Clerodendron trichotomum* Thunb. (14), although there are two separate vascular strands related to a single gap at the nodal level, these strands do not unite at lower levels but retain their individuality and are connected to *two entirely independent bundle systems of the eustele*. This raises the question whether there are two fundamentally different types of vasculature within the Pteropsida or merely extreme deviations from a single basic type.

In *Ginkgo*, the vasculature of the lamina is typically dichotomous, the veins of the two bilateral halves of the leaf being related, however, to two independent parts of the eustele. Therefore, the number of veins tends to be a multiple of two, viz., an *even* number. This is in marked contrast to the vasculature of many dicotyledonous leaves which tend to have an *odd* number of vascular strands at the nodal level. How does a transition from an *even* to an *odd* number of vascular strands occur?

In those representatives of the Coniferales which have a single vascular strand in the leaf and at nodal levels, the vasculature might be due to a suppression of dichotomies correlated with extreme reduction in the breadth of the lamina of the leaf. On the contrary, in dicotyledons which have relatively broad leaves and a single vascular strand at the nodal level, the strand frequently is resolved at subnodal levels into two independent traces. In other words, the single strand at the nodal level may be interpreted as having evolved by *fusion* of *two* independent traces rather than by suppression of the dichotomy of a *single* trace.

In this connection, recent investigations of the Chloranthaceae, Lactoridaceae, Amborellaceae, Trimeniaceae, Austrobaileyaaceae, Monimiaceae,

Lauraceae, Gomortegaceae and Hernandiaceae have revealed considerable significant evidence. The *totality* of morphological characters from different organs and parts indicates that these families are relatively closely related and constitute one of two major categories of the woody Ranales (*sensu lato*). With a few exceptions, which will be discussed subsequently, all of the numerous genera have prevailingly unilacunar nodes and simple leaves with characteristically pinnate venation. The xylem of the various genera exhibits numerous successive evolutionary stages in the development of vessels; that of *Sarcandra* (24) and *Amborella* (2) being of a primitive vesselless form, whereas that of the Hernandiaceae contains vessels of a highly evolved and specialized structure.

In *Ascarina* (22), *Austrobaileya* (3), *Lactoris* (23) and *Trimenia* (16), there are two independent foliar traces which extend upward to the nodal level and into the petiole of the leaf. These vascular strands may remain distinct and separate throughout the costa of the lamina or they may fuse to form a single mid-vein, particularly in the middle and upper parts of the lamina. Thus, each bilateral half of the simple, pinnately veined leaf is vascularized by minor lateral ramifications of an independent foliar trace. In *Amborella* (2) and in certain representatives of the Monimiaceae (16) fusion of the two principal strands to form a single broad arc of vascular tissue extends downward to the nodal level, giving the impression, *except at lower levels*, that the leaf is vascularized by a single foliar trace.

In *Piptocalyx* (16), a close relative of *Trimenia*, the two independent traces tend to dichotomize, forming four strands in their upward course toward the base of the leaf. The two central strands commonly fuse at the nodal level or in the basal part of the petiole, thus exhibiting a transition from an *even* number (four) to an *odd* number (three) of foliar vascular strands. Numerous representatives of the Monimiaceae likewise have an odd number (three, five, seven, nine) of strands at the nodal level. That these strands commonly result from the bifurcation of two independent traces may be demonstrated by tracing them downward through two internodes of the stem. In many cases at least, the odd number of strands at the nodal level is due to the fusion of strands that belong to two independent systems of vasculature. Such a pattern of dichotomy and fusion occurs in many species of *Hedyosmum* (22), where there are usually five strands at the nodal level and in the base of the petiole.

In all of the numerous genera of these families, with the possible exception of *Sarcandra* and *Chloranthus*, there is no evidence which may be interpreted as indicative of the derivation of a unilacunar from a trilacunar form of nodal structure. The occurrence of three strands (as well as one, two, four, five, six, seven or nine) at the nodal level cannot be accepted as unquestionable evidence of a transition to unilacunar vasculature by the approximation of three separate strands of a trilacunar node.

Within the Chloranthaceae (22) *Ascarina*, as previously noted, has two independent traces which pass upward to the nodal level and extend out-

ward through the petiole into the lamina of the leaf. In *Hedyosmum* the two traces divide in their upward course, forming six strands, the two slender central members of which tend to unite at the nodal level. Thus, at this level, the leaf appears to be vascularized by an odd number (five) of primary strands. *Sarcandra* and *Chloranthus* resemble *Ascarina* in having two massive independent traces which extend upward into the leaf. Most of the bilateral vasculature of the pinnately veined lamina is related to these two conspicuous strands. However, the basic pattern of vasculature is complicated in the petiole and at the nodal level by the occurrence of three small additional strands. The medianly located one of these is formed, as in *Hedyosmum*, by the fusion of minor branches of the two subtending leaf traces. The other minor strands are laterally situated and are related to independent traces at separate gaps in the eustele. In most dicotyledons having opposite leaves and trilacunar structure, there are six gaps at the nodal level, i.e., three independent gaps for each leaf, compare *Fig. 1, G*. In *Sarcandra* and *Chloranthus* there are four gaps, two median ones facing the leaves as in *Ascarina* and *Hedyosmum* and two lateral ones in addition. The corresponding lateral strands of the two leaves fuse at the nodal level and are jointly related to these gaps, compare *Fig. 1, F*. However, at lower levels they separate and become attached to independent parts of the eustele. *A priori* there is no convincing evidence for interpreting this aberrant form of vasculature as a transition from trilacunar to unilacunar nodal structure rather than *vice versa*. Indeed, the totality of evidence indicates that there is a fundamental *double* system of vasculature throughout all representatives of this group of families; transitions from an even to an odd number of vascular strands occurring at different levels. Furthermore, it suggests that pairs of independently attached lateral strands may be added without necessarily modifying the number of principal strands that are related to the median gap in the eustele.

There are other categories of dicotyledons where a summation of evidence is indicative of a transition from unilacunar to trilacunar or multilacunar nodal anatomy rather than *vice versa*. For example, a majority of the Ericales are characterized by having simple pinnately veined leaves and unilacunar nodes. However, there is an aberrant tendency in the Epacridaceae, as in the Thibaudieae of the Ericaceae, to form leaves with palmately parallel venation. As emphasized by Dormer (5), only five of the more than twenty genera of the Epacridaceae have leaves with sheathing bases. Two of these, *Richea* and *Dracophyllum*, differ markedly from the rest of the Epacridaceae, and from other representatives of the Ericales, in having trilacunar and multilacunar nodes. Thus, in the case of the Epacridaceae, as of the Chloranthaceae, a *totality* of evidence is indicative of the derivation of trilacunar and multilacunar nodes from a unilacunar one. This is in marked contrast to conditions in such families as the Leguminosae, Anacardiaceae, etc., where certain genera or species exhibit reduction from trilacunar to unilacunar nodes.

A summation of evidence from the dicotyledons as a whole indicates,



therefore, that conspicuous modifications of nodal structure are reversible, pairs of independently attached lateral strands being added in certain cases and eliminated in others. Furthermore, the addition or subtraction of pairs of independently attached strands can occur without fundamental changes in the number of the vascular strands related to the median gap of the node. Thus, more emphasis should be placed in the future upon studying vascular tissues related to the median gap and upon tracing their extensions downward into lower levels of the stem. Transitions from an *even* to an *odd* number of traces appear to be of considerable significance in the phylogeny of the Pteropsida and in discussions of "Telomic" interpretations of vascularization patterns.

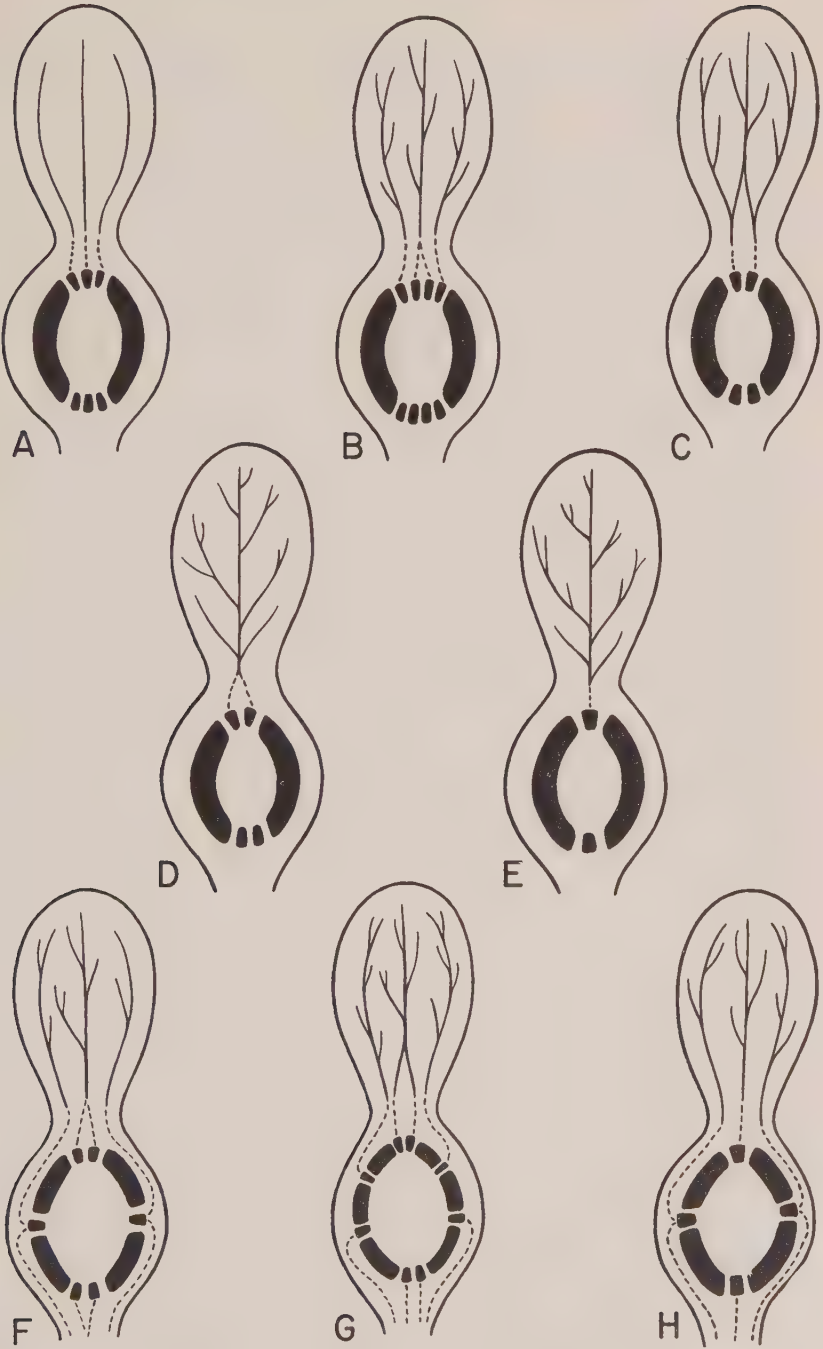
#### DEVELOPMENTAL INVESTIGATIONS

At present there is a dearth of reliable information regarding the extensions of leaf traces below the nodal level. Successive stages in the development of procambium, phloem, and xylem have been investigated by adequate modern techniques in a very limited number of genera and species. However, Nägeli's (17) numerous illustrations, coupled with the detailed investigation of *Linum* by Esau (7, 8) and Girolami (10), of *Sambucus* and *Helianthus* by Esau (9), and my own preliminary studies of a considerable number of dicotyledons, indicate that the leaf trace related to the median gap of the node (when followed downward) frequently forks above the next subtending leaf of an orthostichy. In other words, the halves of the leaf trace are related at lower levels to two independent parts of the eustele. This suggests (from ontogenetic and phylogenetic points of view) a fusion of two independent strands, and does not support telomic illustrations of a single trace which dichotomizes in its upward extension. Furthermore, the lateral traces of trilacunar and multilacunar nodes do not unite in most cases to form a single strand at lower levels.

#### NODAL ANATOMY AND VASCULATURE OF SEEDLINGS

As demonstrated in Lubbock's (13) comprehensive treatment of dicotyledonous seedlings, a majority of their cotyledons are simple and entire. However, there is a wide range of variability in form from broadly elliptical, orbicular, ovate, obovate, cordate or reniform to oblanceolate, spatulate or linear, and from sessile to extensively petiolate. Although palmately lobed, trifid, tripartite or multifid cotyledons are comparatively rare, emarginate, bilobed, bifid and auriculate forms are of not infrequent occurrence in various families.

As emphasized by Lubbock and others, there is a striking difference in form between the cotyledons and leaves of specific seedlings. This is particularly conspicuous in families having serrate, dentate, lobed, cleft, divided or compound leaves. Instances, e.g., Onagraceae, where the cotyledons assume a form during the later stages of their enlargement which



TEXT-FIG. 1. A-H, forms of cotyledonary nodal anatomy in dicotyledons.

closely resembles that of the first-formed leaves, are of exceptional rather than of common occurrence. In other words, although there is a similar range of variability in the form of cotyledons as among leaves, similar forms of cotyledons and leaves rarely occur in close association on the same seedling.

A reconnaissance of seedlings obtained from 99 families of the dicotyledons reveals a range of variability in cotyledonary nodal anatomy that is illustrated in *Fig. 1*. These patterns resemble structures that are known to occur at foliar nodes having opposite leaves. It is significant in this connection, however, that cotyledons with multilacunar attachments are rare, and that the frequency of occurrence of the unilacunar and trilacunar forms differs considerably in the case of cotyledons as contrasted with leaves.

Among cotyledons of the species investigated, 77% have an *even* number of vascular strands at the nodal level (*B*, *C*, *D*, *F* & *G*), and 60% of them have *two* independent traces that are related to a single gap (*C* & *D*). The latter double-trace, unilacunar form of nodal structure is not confined to a few specific genera, but evidently is of common occurrence in many orders and families of the dicotyledons. This is in marked contrast to foliar nodes where a large majority of dicotyledonous leaves are reported to have an *odd* number of traces and where the double-trace unilacunar form of structure has been encountered thus far in a limited number of families, viz., certain representatives of the Austrobaileyaceae, Trimeniaceae, Chloranthaceae, Lactoridaceae, Verbenaceae, Labiatae and Solanaceae.

Of the cotyledonary nodal patterns illustrated in *Fig. 1*, (*B*), present in 7% of the seedlings investigated, and forms (*F*) and (*G*), in 10% of them, are apparently of infrequent occurrence at foliar nodes. Form (*B*) has, however, been encountered at certain of the foliar nodes of *Piptocalyx* and form (*F*) at those of *Sargentodoxa*. On the contrary, form (*A*), having *three* strands related to a single gap, is of less frequent occurrence at cotyledonary nodes although commonly encountered at foliar ones.

In the case of leaves arranged in an opposite or decussate phyllotaxy and having one pair of independently attached lateral vascular strands, there usually are, as previously stated, six gaps at the nodal level, viz., three related to each of two leaves. Although this type of structure occurs at times at cotyledonary nodes (*G*), it is much less common than the arrangement illustrated in patterns (*F*) and (*H*) where the corresponding laterals of the two cotyledons unite and are related to two, instead of to four, independent lateral gaps. Although uncommon, this modification of trilacunar structure occurs as previously stated at the foliar nodes of *Chloranthus* and *Sarcandra*, and has been encountered at those of certain representatives of other families, e.g., Rubiaceae.

Thus, a reconnaissance of seedlings indicates that there is a range of structural variability in cotyledonary nodes similar to that found in foliar ones. The fundamental differences between the vasculature of leaves and cotyledons at the nodal level are quantitative rather than qualitative, an



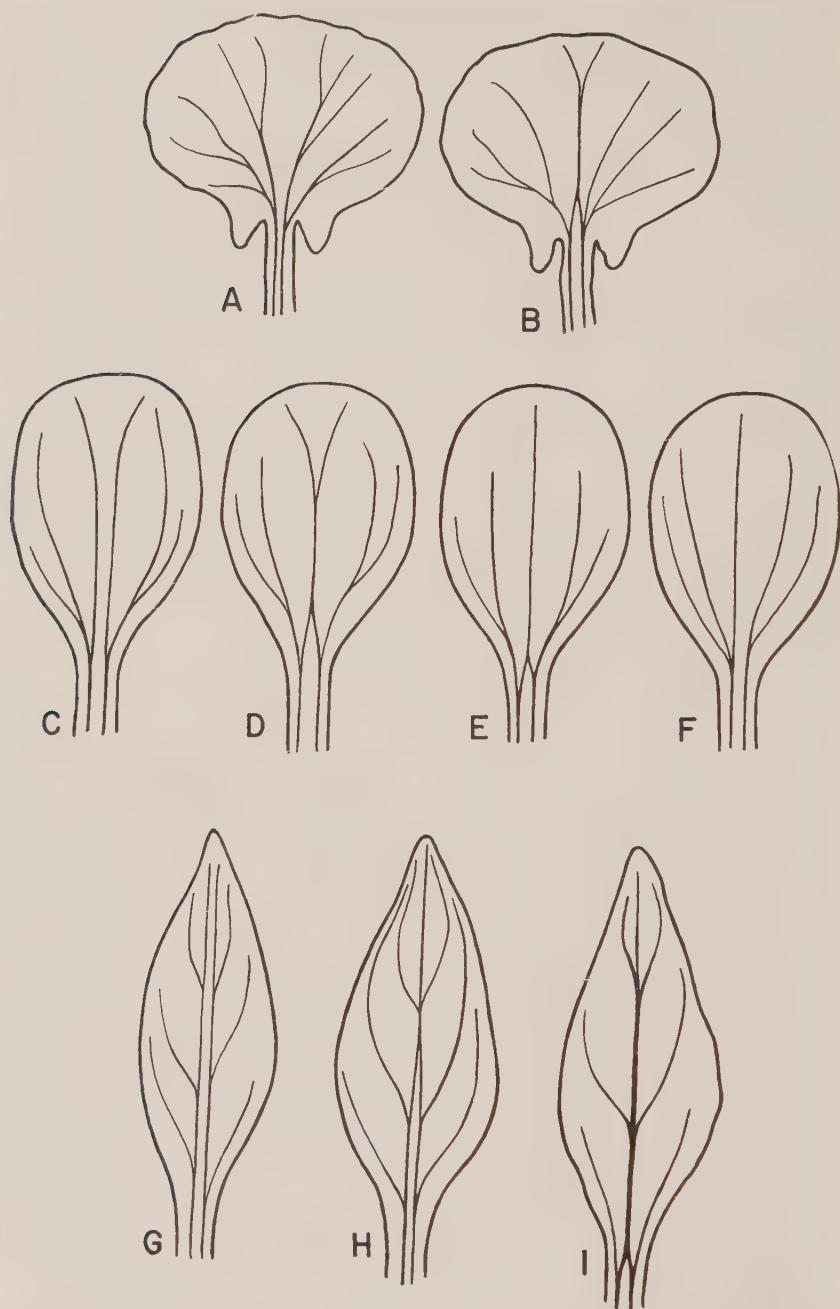
*even* number of vascular strands being commoner in the case of cotyledons and an *odd* number in the case of leaves

It should be noted in this connection, however, that cotyledons with multilacunar attachments do not occur in any of the seedlings that I have studied, even in families where the leaves of adult plants are attached at multilacunar nodes. Although cotyledons with pentalacunar vasculatures have been demonstrated by Carlquist (4) to occur in *Fitchia speciosa* Cheeseman, there are reasons for believing that multilacunar attachments will prove to be of infrequent occurrence in the dicotyledons as a whole. In families having multilacunar foliar nodes, e.g., Magnoliaceae, Polygonaceae, Umbelliferae, etc., the leaves are arranged prevailingly in alternate rather than in opposite phyllotaxy. There appear to be spatial and other difficulties in the development of multilacunar nodes where the leaves are opposite. Furthermore, as previously noted, where the leaves of adult plants are multilacunar the first leaf of the seedling commonly tends to be trilacunar with transitions to the typical adult multilacunar condition occurring in subsequently formed leaves of the young plant. The cotyledonary nodes of such plants are either of the unilacunar type (viz., having two gaps, one for each of the opposite cotyledons) or of the trilacunar forms illustrated in (*F*), (*G*) and (*H*). In this respect, the seedlings of such plants with multilacunar foliar nodes resemble those of the multilacunar living cycads and *Gnetum*.

It should be emphasized in this connection that, if the trilacunar condition is primitive in angiosperms, and if the ontogenetic sequences in the preceding paragraph are to be interpreted as recapitulations of the phylogenetic derivation of multilacunar nodes from trilacunar ones, then one might anticipate finding ontogenetic sequences in seedlings illustrating the reduction of trilacunar nodes to unilacunar ones. Although a considerable number of seedlings that I have examined have a first-formed leaf attached at a unilacunar node in contrast to the trilacunar or even the multilacunar nodes of the adult plant, I have not succeeded thus far in finding a succession of seedling leaves which exhibit an ontogenetic transition from trilacunar to unilacunar structure.

As previously emphasized by Sinnott and myself (21), many cotyledons are characterized by having a pseudo-palmate or palmate-parallel venation. In such cotyledons, there commonly are three or five conspicuous primary veins that extend outward from a locus at the base of the cotyledon, the lateral ones diverging and extending parallel to the margins of the lamina, *Fig. 1, C, Fig. 2, E*. A large number of these cotyledons show a transition from an *even* number (two) of vascular strands at the nodal level to an *odd* number (three or five) of primary veins in the lamina. The outward extensions of the two independent traces commonly divide in the petiole or the base of the lamina, forming four or six strands, the two central members of which unite to form a mid-vein, *Fig. 2, E*.

There are numerous deviations and aberrations of this common form of pseudo-palmate vasculature, not only among different families and genera, but also among seedlings of the same genus or species. The branches of



TEXT-FIG. 2. A-I, forms of cotyledonary venation in dicotyledons.

the two traces may remain independent throughout the lamina, *Fig. 2, A & C*, or the two central ones may approximate and then diverge toward the apex of the cotyledon, *Fig. 2, D*. Where the branching is symmetrical, *Fig. 2, A & C*, there is an *even* number of conspicuous veins in the lamina. On the contrary, where the branching is asymmetrical, as sometimes happens, *Fig. 2, F*, a single branch of one trace may assume the position of a mid-vein, and there may be an *odd* number of conspicuous veins in the lamina.

The phenomena of dichotomy and fusion, which lead to a transition from an even to an odd number of vascular strands, may occur at different levels of the lamina, the petiole or the nodal and subnodal regions. Where the dichotomy is precocious, there may be four or even six strands related to a single gap at the nodal level, *Fig. 1, B*. Conversely, where the concrescence of independent strands is precocious, there may be a single strand at the node, *Fig. 1, E*, or in the petiole, *Fig. 1, D*, with one, three or five conspicuous veins diverging from it in the base of the lamina. Where both dichotomy and concrescence are precocious, there may be three strands related to a single gap at the nodal level, *Fig. 1, A*. In the case of cotyledons having more than two strands at the level of attachment, two or more of the basal lateral veins of the lamina commonly are in direct continuity with independent traces, related either to a single gap, *Fig. 1, A & B*, or to independent lateral gaps, *F, G, & H*.

It should be noted in this connection that there are numerous cotyledons which exhibit intermediate or transitional forms of vasculature between these pseudo-palmate patterns and typically pinnate ones. In such cotyledons, the basal lateral veins are less conspicuous and extensive and the apical branches of the mid-vein are correspondingly emphasized, *Fig. 2, H & I*. It is significant, however, that even the narrower forms of pinnately veined cotyledons commonly exhibit a vasculature that is related at some level to two independent vascular strands or traces. As in the pinnately veined leaves of *Austrobaileya*, *Trimenia* and *Ascarina*, two traces may extend independently throughout a cotyledon, *Fig. 2, G*, or they may become concrescent at varying levels of the lamina, *Fig. 2, H*, of the petiole, *Fig. 2, I*, or of the node, *Fig. 1, E*.

There appears to be no conspicuous and universal correlation between the form and venation of cotyledons and specific types of nodal structure. Cotyledons of widely varying form and venation may have a similar basal vasculature. Conversely, cotyledons of similar form may be attached at strikingly different nodes. However, there does appear to be a higher percentage of pinnate venation among cotyledons which are attached at single-trace unilacunar nodes.

Occasionally there is a considerable range of variability in the vasculature of cotyledons grown from the seed of a single plant, and at times in the two cotyledons of a single seedling. For example, one cotyledon may have four vascular strands related to a single gap at the nodal level, *Fig. 1, B*, whereas the opposite cotyledon has one or two of these strands attached at independent gaps, *Fig. 1, G*. The branches of two traces



may extend independently throughout the lamina of one cotyledon, *Fig. 2, A, C, F & G*, whereas approximation and concrescence of branches to form a mid-vein occur in another cotyledon, *Fig. 2, B, E, H & I*.

#### VASCULATURE OF FLORAL APPENDAGES

The nodal anatomy of floral bracts, bracteoles, and the independent parts of polysepalous calyces frequently resembles that of the leaves of the plant upon which the flowers are borne. However, there are numerous deviations, and the venation of free sepals, as of petals, tends in many cases to be pseudo-palmate even where the leaves have a typical pinnate venation. The folded megasporophylls of apocarpous flowers also tend to have a palmate-parallel venation, the basal vasculature varying from unilacunar to trilacunar to multilacunar. According to Eames (6), the 3-veined (one dorsal and two ventrals) trilacunar form of carpel is primitive, the unilacunar and multilacunar forms having developed from it by obvious trends of simplification and amplification. Most stamens have a single vascular strand that is related to a unilacunar node.

Recent investigations of a number of the less well known tropical and subtropical representatives of the woody Ranales (*sensu lato*) have revealed evidences of what appear to be primitive forms of floral morphology. Among such plants there are various stages in the differentiation of sterile appendages into bracteoles, sepals and petals. There are broad microsporophylls which are not differentiated into filament, anther and connective, and unsealed, styleless megasporophylls with widely diffused stigmatic surfaces.

The carpels of the less specialized flowers of the Winteraceae resemble conduplicately folded, emarginate, pseudo-palmate, 3-veined cotyledons. The microsporophylls and staminodes of *Degeneria* and *Himantandra* also have a palmate-parallel, 3-veined vasculature, as do many of the stamens of the Magnoliaceae. Such occurrences strengthen Eames's contention that primitive carpels and stamens were conspicuously 3-veined sporophylls. In the case of carpels, the elimination of a stipe, incipient adnation to the torus, sterilization of the upper part of the megasporophyll as a concomitant of the formation of a style, reduction in the number of ovules, and diverse forms of adnation and cohesion tend more or less extensively to modify this primitive vasculature. In the case of the stamen, reduction in the lamina of the microsporophyll, increasing protuberance of the sporangia, and the formation of a comparatively slender filament appear to have resulted in the suppression and elimination of the lateral veins, leaving a single median vascular strand.

Although the venation of relatively primitive forms of carpels and stamens tends to be comparatively stable within a flower, their vasculature at nodal and subnodal levels commonly is variable even in a single specimen, as might be anticipated from a developmental point of view where numerous appendages are congested upon the broadened apex of a pedicel. The three principal veins of one carpel or stamen may be

related to a single trace (unilacunar) at the nodal level, those of another may be related to three approximated traces (unilacunar), whereas those of a third are related to three widely separated traces (trilacunar).

Transitions from an even (two or four) to an odd (one or three) number of vascular strands are apparently of infrequent occurrence even in the subnodal levels of floral axes. However, in *Austrobaileya* (3) the dorsal vein of the carpels, the mid-vein of the broad microsporophylls, and the veins of the staminodia, tepals and bracteoles are related at lower levels to two separate traces which are related in turn to two separate parts of the eustele. Furthermore, in the case of *Sarcandra* (24), a vesselless representative of the Chloranthaceae, there is a single stamen that is basally adnate to a carpel. The mid-vein of the stamen usually is double. Not only may the paired veins run independently throughout the stamen, but also they are related at lower levels to two independent bundles of the eustele. Transitions from *two* independent strands to *one* occur at times and at different levels by concrescence of the two strands. The carpel of *S. glaber* has a double dorsal vein and two ventrals which may be widely separated or closely approximated. The carpel of *S. hainanensis*, on the contrary, not only has a single dorsal vein, but also a single ventral one due presumably to the concrescence of two ventral veins or to the suppression of one of them.

Although detailed developmental investigations are likely to reveal additional instances of doubleness in the subtending traces of floral appendages, it is unlikely that transitions from an even number of traces to an odd number of principal veins will prove to be of as frequent occurrence in the case of stamens and carpels as in the case of leaves and particularly of cotyledons.

It should be noted in these connections that cotyledons and floral appendages are of comparatively limited size, and rarely, if ever, have stipules or a truly compound lamina. Furthermore, where they have the homologue of a petiole, the vasculature does not attain the extreme complexities that occur in the petiole and costa of many leaves. With the exclusion of compound leaves and excessive petiolar complexities, one finds a similar range of potentialities of form and vasculature in cotyledons and floral appendages as in simple leaves with pinnate or palmate venation. The differences between various categories of appendages are quantitative rather than qualitative. Two-trace unilacunar nodes and transitions from an even to an odd number of vascular strands are apparently of decreasing frequency in passing from cotyledons to leaves to stamens and carpels.

## DISCUSSION

The data recorded on preceding pages indicate that it is no longer possible to assume that unilacunar nodes in dicotyledons are derived *in all cases* by reduction from a trilacunar condition. Although reduction of trilacunar nodes to unilacunar ones in dicotyledons may ultimately prove

to be of more common occurrence than the reverse phenomenon of amplification from unilacunar to trilacunar, this can be determined with certainty only by more comprehensive and laborious investigations of individual families and orders.

A summation of extensive evidence from the Ranales (*sensu lato*) suggests that during early stages of the evolution and diversification of the dicotyledons, or of their ancestors, certain of the plants developed trilacunar nodes, whereas others retained the primitive unilacunar structure that occurs so characteristically in ferns, seed ferns, Bennettitales (*sensu lato*), Cordaitales, Coniferales, *Ginkgo* and *Ephedra*. Furthermore, a broad survey of seedlings of both dicotyledons and monocotyledons — as well as of those of the living cycads and *Gnetum* — indicates that, where adult plants have developed trilacunar and multilacunar nodes, the cotyledons and first juvenile leaves commonly exhibit a retardation or inhibition of the tendency to form one or more pairs of independently attached lateral traces.

In addition, a summation of seedling evidence accentuates the significance of the occurrence of two independent systems of foliar vasculature in such dicotyledonous families as the Austrobaileyaceae, Trimeniaceae, Chloranthaceae and Lactoridaceae. It necessitates a re-evaluation of the "Theory of the double leaf trace" briefly outlined in 1907 by Thomas (25).

It should be emphasized in this connection that the double-trace unilacunar form of vasculature of leaves, *as of buds*, is significant from physiological, as well as from morphological points of view. An actively transpiring appendage with this form of attachment is able to tap more conducting tissue of the primary body of the main axis than it would be able to do if connected to a single vascular strand at lower levels of the eustele. Transitions from unilacunar to trilacunar and multilacunar structures not only insure more numerous contacts with the conducting strands of the eustele of the stem, but also can provide mechanically stronger attachments at the nodal level.

It is of interest, accordingly, to inquire whether a double-trace pattern of vasculature is a primitive basic form in Pteropsida from which others have been derived by various trends of structural modification. Does a single-trace unilacunar structure arise in all cases by the approximation and fusion of two originally independent vascular strands? Data obtained from nodes and leaves of adult shoots, without reliable information regarding the development and attachment of leaf traces in subnodal parts of the stem, are inadequate for fully answering the question. Although the vascular tissues related to unilacunar nodes, and to the median gap of trilacunar ones, have been demonstrated in an increasing number of cases to be related at lower levels of an orthostichy to two independent parts of the eustele, it is not known at present whether such attachments predominate in the dicotyledons and in various categories of the gymnosperms. Nor is there reliable evidence to indicate how extreme reductions in the size of leaves, and various xerophytic adaptations, may modify patterns of vasculature. However, reductions of trilacunar to unilacunar nodes



appear in certain dicotyledonous families to be correlated with such modifying factors. Accurate developmental investigations of the Coniferales may prove to be particularly significant in studying the effects of xerophytic tendencies.

It should be noted in passing that the vascular tissues of the primary body are described in terms of steles, bundles, traces and veins. However, in growing shoots of dicotyledons, the leaf traces are composed of long files of vertically contiguous tracheary cells. The individual files may be in contact laterally or they may be separated by parenchymatous elements. During the earlier stages of growth (after the acropetal development of the procambium) they differentiate successively from loci in the base of the leaf, and eventually extend from the lamina of the leaf downward through a varying number of internodes of the stem. From the point of view of translocation, they provide convenient precursors in the development of vessels. Furthermore, even when aggregated in a single trace, they provide independent channels of rapid movement into each bilateral half of a leaf. Thus, traces and veins may be regarded as aggregations of independent channels of rapid translocation, rather than as the most significant units in a system of conduction.

As previously stated, Sinnott and I (21) concluded that the primitive angiospermic leaf was simple, palmately veined, probably 3-lobed, and was provided with three main veins which were attached at a trilacunar node. The occurrence in certain dicotyledonous families of transitions from unilacunar to trilacunar structures and from pinnate to palmate-parallel venation indicates that the evolution of leaf form and vasculature is not a strictly unidirectional and irreversible phenomenon as in the case of the phylogeny of the angiospermic vessel. Furthermore, although relatively primitive forms of carpels and stamens have three conspicuous primary veins, evidence from cotyledons and from the leaves of a number of ranalian and other families raises the possibility that the mid-vein of angiospermic appendages may have evolved by the approximation and fusion of branches of two independent systems of vasculature. However, it should be freely admitted in conclusion that critical paleobotanical evidence is not available as yet for solving the problem of the ancestry of the angiosperms or of the primitive form and vasculature of their appendages.

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STUDIES IN THE BORAGINACEAE, XXVIII.  
NEW OR OTHERWISE INTERESTING SPECIES FROM  
AMERICA AND ASIA

IVAN M. JOHNSTON

*Cordia* (§ *Varronia*) *lauta*, sp. nov.

Frutex 1.5–2 m. altus; ramulis 5–7 mm. crassis antrorse fulvo-strigosis (pilis ca. 1 mm. longis); foliis ellipticis evidenter venosis 8–12 cm. longis 5–7 cm. latis medium versus vel paulo infra medium latissimis utroque angulatis, margine evidenter irregulariterque serratis, supra fulvescentibus abundanter strigosis (pilis rectis 0.5–1 mm. longis e basibus disciformibus ca. 0.2 mm. diametro erumpentibus), subtus pallidioribus juventute plus minusve tomentulosis (pilis curvatis vel subtortuosis albis vel griseis gracilibus plerumque ca. 0.5 mm. longis); petiolis crassis 5–10 mm. longis fulvo-strigosis; pedunculo perelongate 10–30 cm. longo 3–4 mm. crasso terminali vel internodali; inflorescentia capitata ante anthesin 3–3.5 mm. diametro; calyce in alabastro obovoideo 12–16 mm. longo apicem versus 7–8 mm. crasso supra medium strigoso sessili, lobis triangularibus 4–4.5 mm. longis basi 3–4.5 mm. latis acutis fere ad apicem appendiculis liberis crassiusculis ad 1.5 mm. longis donatis; corolla conspicua alba infundibuliformi 6.0–7.8 cm. longa glaberrima 6–7-mera, limbo 4–5 cm. diametro; lobis ad 20 mm. latis ad 5 mm. longis rotundis vel subtruncatis, tubo ad 3 cm. longo nervis validis 12 vel 14 donato basi imo ca. 5 mm. crasso 1.5–2 cm. supra basim ca. 3 mm. crasso deinde sursum ampliato; staminibus 6–7 inclusis; antheris 4 mm. longis ad 1 mm. latis paulo infra medium affixis basi 1.5–7 mm. profunde lobatis apice emarginatis, supra medium connectivo lato encrassato donatis; filamentis 30–35 mm. longis filiformibus 3–3.5 mm. supra basim corollae affixis, ca. 1–5 mm. infra basim sinuum limbi corollae attingentibus; pollinis sphaericis ca. 160  $\mu$  prominenter abundanterque papillatis et minute punctulatis oribus circularibus 3 donatis; stylo 75–80 mm. longo e corolla breviter exserto, apice ca. 2.5 mm. profunde lobatis, lobis ca. 1 mm. profunde lobulatis; stigmatibus 4 capitatis terminatis; fructu ignoto.

MEXICO: Plan de Barrancas, Jalisco, steep rocky volcanic slopes, 2500–3500 ft. alt., shrub 1.5–2 m. tall, with white flowers, July 17, 1951, *H. S. Gentry & C. L. Gilly 10878* (TYPE, Arn. Arb.).

A species notable for its robust habit, coarse, very elongate peduncles, large calyces, and very large corollas. The corollas are certainly the largest known in the section *Varronia* and, furthermore, are larger than those of any other American member of the genus *Cordia*. The pollen is notable for its large size and its verrucose surface. Relationships of the species are uncertain. It must be classified with those *Varronias* having distinctly

capitate, terminal or extra-axillary inflorescences and simple, non-stellate indument. It has, however, no evident relationship with any of the members of that assemblage either north or south of the Equator. The species is one of the most distinct members of its genus that has been discovered in America during the past quarter century.

***Cordia salvifolia* Juss. ex Poir. Encyc. 7: 46 (1806).**

*Cordia Buchii* Urban, Symb. Ant. 1: 475 (1900).

The type of *Cordia salvifolia* is in folder no. 6476 of the Jussieu Herbarium at Paris. A recent examination of the specimen reveals it to be a sterile branch of the endemic species of the island of Hispaniola which Urban described under the name *Cordia Buchii*. It does not represent the shrub of the Lesser Antilles which has been accepted as "*Cordia salvifolia*" for over a century. The label associated with Jussieu's type bears only the following data: "*Cordia salvifolia* J., donne par M. Dupuis".

***Cordia* (§ *Varronia*) *nesophila*, sp. nov.**

Frutex 1–3 m. altus; ramis hornotinis 2–4 mm. crassis strigosis (pilis rigidis 0.1–0.4 mm. longis); foliis lanceolatis vel elliptico-lanceolatis 5–12 cm. longis 2–5 cm. latis, apice acutis, basi acutis vel plus minusve rotundis in petiolum 8–12 mm. longum abrupte contractis, margine dentatis vel dentato-crenatis, in facie superiore scabridis (setis minutis rigidis ascendentibus vel appressis e basi incrassata vel discoidea erumpentibus 0.1–0.5 mm. longis), in facie inferiore pallidioribus (pilis tenuioribus mollibus brevibus curvatis secus nervos gestis); nervis foliorum supra impressis, subtus prominentibus, primariis utroque latere costae 8–14 sub angulo ca. 45° abeuntibus vix vel parvum arcuatis, secundariis et tertiariis areolato-anastomosantibus; inflorescentia laxa ascendentique dichotoma corymbosa 3–6 cm. lata multiflora 1–5 cm. longe pedunculata in ramis hornotinis terminali; calyce campanulato ca. 3.5 mm. longo, lobis deltoideis ca. 1 mm. longis nullo modo appendiculatis; corolla alba, 5.5 mm. longa tubulosa; lobis ascendentibus rotundis erosis et crispis saepe ca. 2 mm. longis et 2 mm. latis; tubo ad 2 mm. crasso, intus solum secus nervum infra insertionem staminum positum inconspicue villuloso; staminibus inclusis; filamentis 0.2–0.8 mm. longis 1.7–2.8 mm. supra basim corollae affixis; antheris 1–1.5 mm. longis; stylo 2–2.5 longo calyce vix exserto; endocarpio maturitate subgloboso 3–5 mm. longo.

WEST INDIES: St. Lucia, Dauphin, *P. Beard* 1080 (G); Martinique, St. Anne, *Stehlé* 6161 (A); Martinique, *Duss* 287 (G); Guadeloupe, Anse—Bertrand, *Stehlé* 2698 (G), 2689 (G); Marie-Galante, Capesterre, *H. Stehlé* 2678 (TYPE, Gray Herb.); Antigua, *Rose, Fitch & Russell* 3339 (G); Barbuda, near Codrington Village, *Box* 613 (G).

The plant described above is the well known and unmistakable species of the Lesser Antilles which for nearly a century and a half has been

accepted as "*Cordia salvifolia*". The most recent treatment of it is to be found in my account of the "Boraginaceae of the Southern West Indies", Jour. Arn. Arb. 30: 117 (1949). Unhappily, study of the historic specimens at Paris has revealed that the name *C. salvifolia* Juss. ex Poir. Encyc. 7: 46 (1860) applies not to the present species but rather to the very different *Cordia Buchii* Urban (1900), of adjacent southern portions of Haiti and Santo Domingo. Since our plant has no available legitimate name a new one must be proposed.

***Cordia* (§ *Varronia*) *lippoides*, sp. nov.**

Frutex; ramis hornotinis ca. 10 cm. longis ad 2 mm. crassis hispido-villulosis (pilis 0.5–1 mm. longis); foliis ovatis vel ellipticis 1–2 cm. longis 8–14 mm. latis, basi abrupte acutis in petiolum ca. 2 mm. longum attenuatis, margine crenatis, supra viridibus areolato-bullatis scabris, subtus pallidis nervosis villosis; inflorescentia in ramis terminali vel laterali et oppositifoliata dense hemispherica vel subglobosa 16–20 mm. diametro 15–20-flora 1–2.5 cm. longe pedunculata; calyce sub anthesi 5.5–9 mm. longo supra medium lobato, in alabastro obovato ad 3 mm. crasso apice appendiculas 5 setaceas 1–2 mm. longas liberis terminato; lobis calycis longe subulateque productis, apice setaceis flexuosis hispidulis (pilis saepe brunneis 0.3–0.8 mm. longis); corolla late tubulosa 6.5 mm. longa apice ca. 5 mm. crassa basi ad 2.5 mm. diametro, intus infra insertionem filamentis villulosa, limbo subintegro; filamentis 2–2.5 mm. longis subulatis ca. 3.5 mm. supra basim corollae affixis; stylo 5.5 mm. longo, lobis spathulatis ca. 1 mm. longis; drupa rubra, endocarpio irregulariter elliptico-ovoideo 6 mm. longo 3 mm. crasso.

PERU: Conay, abajo de Chiquián, dept. Ancash, prov. Bolognesi, monte pluvifolio, 2600 m. alt., May 12, 1950, *Emma Cerrate* 565 (TYPE, Gray Herb.).

Most closely related to *C. lantanoides* Spreng. (*Varronia crenata* R. & S.), which it closely resembles in foliage and gross habit. It differs from that species, however, in having not only a very much larger calyx but also one in which the lobes have very prolonged tips which are free and flexuous in the bud.

***Cordia* (§ *Varronia*) *munda*, sp. nov.**

Frutex 12–15 dm. altus; ramis hornotinis 4–10 cm. longis 1–1.5 mm. crassis saepissime simplicibus hispidulo-villulosis (pilis saepe brunneis rectis ascendentibus vel divaricatis 0.5–1 mm. longis); ramis vetustioribus cicatriculas foliorum delapsorum prominulas proferentibus; foliis ovatis vel late lanceolatis 20–45 mm. longis 10–20 mm. latis, apice acutis, basi acutis in petiolum gracilem 2–4 mm. longum contractis, margine crenatodentatis, supra viridibus pilis rigidulis laxe adpressis vestitis, subtus strigosis; nervis utroque latere costae 5–6 sub angulo ca. 45° abeuntibus curvatis; inflorescentia dense capitata saepe ca. 12 mm. diametro in ramis



terminali graciliter 3–8 cm. longeque pedunculata, calyce 6–7 mm. longo campanulato pilis brunneis 0.5–1 mm. longis gesto, lobis acutis triangularibus valvatis 1.7–2.5 mm. longis; corolla alba conspicua infundibuliformi ca. 25 mm. longa, limbo ascendenti 25–30 mm. diametro, lobis rotundis 7–10 mm. longis, tubo 5–6 mm. longo 2.5–3.5 mm. crasso in zona 1–3 mm. supra basim corollae posita sparse villosa; filamentis subulatis 2–2.5 mm. longis 4.5–6.5 mm. supra basim corollae in altitudinibus diversis affixis, antheris 1.3 mm. longis; stylo 4 mm. longo, lobis 1.5 et 1 mm. longis; fructu ignoto.

PERU: abajo de Aiza, entre Catahuasi y Tupe, dept. Lima, prov. Yauyos, monte subxerófilo, fl. blancas, muy vistosas, 2300 m. alt., Jan. 30, 1952, *Emma Cerrate & O. Tovar 1294* (TYPE, Gray Herb.).

A member of the section *Varronia* which has an indument of simple (non-stellate) hairs and a terminal inflorescence that is decidedly capitate. The attractive large white infundibuliform corollas have an evidently lobed limb. The calyx-lobes are triangular and have merely an acute apex. The calyx in the bud, accordingly, is rounded on the summit and is not at all terminally appendaged. The species is probably most closely related to *C. Bridgesii* (Fresen.) Johnston, of Bolivia, from which it differs in the much larger, more deeply lobed corollas, the unappendaged calyx, and the larger leaves.

### *Cordia* (§ *Varronia*) *Vargasii*, sp. nov.

Frutex 15–30 dm. altus; ramis hornotinis 5–25 cm. longis ad 4 mm. crassis velutinis (pilis brunneis 0.5–0.89 mm. longis); ramis annotinis glabratiscicatricis foliorum delapsorum prominentis 1–2 mm. altas proferentibus; foliis ovatis vel ovato-ellipticis paulo asymmetricis 3–10 cm. longis 2.5–5.5 cm. latis, basi obtusis vel rotundis in petiolum 4–6 mm. longum abrupte contractis, apice late acutis, margine evidenter serratis, facie superiore pilis rectis rigidulis 0.4–0.8 mm. longis obsitis, subtus hispidulovillulosis pallidioribus; nervis primariis foliorum validis aliquando apicem versis furcatis, utroque latere costae 5–7 donatis, nervis secundariis evidentibus numerosis eos primarios conjunctibus; inflorescentia dense capitata 15–23 mm. diametro in ramo hornotino terminali et interdum ex axillis foliorum superiorum rami oriente 2–8 cm. longe pedunculata; calyce anguste campanulato to 5–7 mm. longo apicem versus 4 mm. crasso supra medium pilos brunneos dense proferente in alabastro breviter crasseque apiculato; corolla 5.5–7 mm. longa ut videtur flava tubulosa quam calyce ca. 2 mm. longiore, intus in zona ca. 1 mm. lata infra insertionem staminum posita villosa, basi tubo 1.5–2 mm. crasso, limbo 3–4 mm. crasso, lobis inconspicuis erosis plus minusve rotundis recurvatis ad 1.5 mm. latis et 0.7 mm. longis; filamentis 1.5–2 mm. longis 3–4.5 mm. supra basim corollae affixis; antheris ellipticis ca. 1 mm. longis vix exsertis; stylo aut 2–3 mm. longo et in calyce incluso aut ca. 5 mm. longo et calyce exserto, lobis 0.5–1 mm. longis; fructu ignoto.

PERU (dept. Cuzco): Aobamba, prov. Convención, 1600–1700 m. alt., Nov. 23, 1950, *C. Vargas* 9790 (TYPE, Gray Herb.); Amaibamba, prov. Convención, Dec. 29–30, 1948, *C. Vargas* 7514 (G); Machupicchu, Oct. 1931, *F. L. Herrera* 3227 (G).

This plant has many-flowered, very dense, capitate inflorescences borne on naked peduncles that terminate the leafy stems and sometimes also arise from the upper-most leaf-axils. The leaves are ovate and in form and size are reminiscent of the foliage of *C. spinescens* L. (= *C. ferruginea* Lam.) but differ from it in having petioles which are not decurrent on any subtended peduncle. The closest relationships of *C. Vargasii* appear to be with *C. axillaris* Johnston, of eastern Brazil and the Amazon headwaters of northern Peru (Alto Rio Huallaga, *Klug* 4385). From that species it differs in its ovate (rather than lanceolate) leaves, its less copious indument of shorter hairs, its more elongate, larger calyces, and its prevailingly terminal heads of flowers.

***Cordia Gharaf*** (Forsk.) Ehrenb. ex Asch., Sitzung.-Berichte Ges. Naturf. Freunde Berlin 1879: 46 (1879) & Verhandl. Bot. Verein Brandenb. 21<sup>2</sup>: 69 (1880); Muschler, Manual Fl. Egypt 2: 781 (1912).

*Cornus Gharaf* Forsk. Fl. Aegypt.-Arab. pg. xcix (1775).

*Cornus sanguinea* Forsk. Fl. Aegypt.-Arab. 33 (1775), not *Cornus sanguinea* L. (1753).

*Cordia sinensis* Lam. Tab. Encyc. 1: 423 (1791); Johnston, Journ. Arn. Arb. 32: 11 (1951).

*Cordia Rothii* R. & S. Syst. 4: 798 (1819).

*Cordia subopposita* DC. Prodr. 9: 480 (1845).

The identity of *C. sinensis* Lam. (1791) has long remained a mystery and there are numerous guesses recorded in the literature as to what species and genus it might represent. During a recent visit to Paris I took the opportunity to examine the type specimen in Lamarck's herbarium. Much to my surprise I found the plant to be the very distinctive desert shrub, *Cordia Gharaf* (Forsk.) Ehrenb., which occurs in Pakistan and western India and also in the deserts of Arabia and eastern Africa. The eastern form of the species, that found in India and Pakistan, was formerly distinguished as *Cordia Rothii* R. & S. The plant does not grow in China nor is it to be expected there. The geographic data associated with the type of *Cordia sinensis* Lam. are accordingly false and misleading. Sonnerat, the collector of the type, must have found the plant in western India.

The name *Cordia Gharaf* currently appears to be generally accepted as the proper name for the present species. Its claims for acceptance, however, are somewhat questionable. The basionym, *Cornus Gharaf*, was not described by Forskål. It is mentioned six times (on pages xci, xciii, xcv, xcvi, xcvi and xcix) in the prefatory portions of his book concerned with the plants of Yemen and there only as a name in lists of economic plants. It is always a bare name except on pg. xcix where, in a list of medical

plants, it is given as follows: "*CORNUS gharaf*. C. II. 10. In cephalalgia." The symbols (C. II. 10.) refer to Centuria II, species no. 10, or in other words to the main body of Forskål's book in which species are described and given individual treatment. The particular reference is to the account of *Cornus sanguinea* of pg. 33. *Cornus sanguinea* Forsk. and the nomen nudum *Cornus Gharaf* Forsk., are alternate equivalent names for one and the same species. The reference on pg. xcix is evidence of this. Indicative also is the fact that all the economic uses attributed in various lists to *Cornus Gharaf* are all mentioned again in the paragraph in which *Cornus sanguinea* is described and its properties enumerated. Although the binomial *C. Gharaf* is not cited as a synonym in the account of *S. sanguinea*, the vernacular "gharaf" is given as a name applied to the plant at Hodeida, Yemen. It seems likely that the binomial *Cornus Gharaf* was intended as only a temporary appellation, perhaps for use by Forskål during his field work. Although used in his notes, it was one which he subsequently planned to replace with the name *Cornus sanguinea*. In the posthumous editing of his manuscripts by Niebuhr, the preliminary name was not altered, with the result that two names for the species were published.

The two binomials published in Forskål's "Flora Aegyptiaco-Arabica" are the oldest ones applied to the *Cordia* in which we are interested. Of these, *Cornus sanguinea* Forsk. (1775) is a later homonym of *Cornus sanguinea* L. (1753) and must be rejected. Being illegitimate it can not serve as a basionym and the specific epithet is not available for transfer to *Cordia*. Accordingly only *Cornus Gharaf* Forsk. is available as a possible basis for a binomial combination under *Cordia*. As I have indicated, even the validity of this name is open to possible challenge. A case against its acceptance can be made on the grounds that obviously it is a temporary, provisional or alternative name which the author did not intend to retain and would not have published had he lived to edit and publish his own manuscript. Nevertheless the binomial actually is published and on pg. xcix of Forskål's book is associated with a description of a plant printed on pg. 33 of the same volume. The minimum requirements for valid publication of the name *Cornus Gharaf* seem to be fulfilled. This is desirable, for otherwise *Cordia Gharaf* (Forsk.) Asch. would not be the valid correct name for our plant and the obscure, long-confused species with the inappropriate name *Cordia sinensis* Lam. would have to be accepted in its stead.

### **Bourreria Rowellii, sp. nov.**

Arbor ad 4–5 m. alta; foliis oblanceolatis 5–7 cm. longis 16–22 mm. latis nervosis (nervis ramosis utroque lateris costae 5–8) supra medium latoribus deinde deorsum gradatim attenuatis, basi acutis, apice obtusis, facie superiore glabris vel solum secus costam sulcatam sparsissime inconspicuissimeque villulosis, facie inferiore pallidioribus leviter appressovillulosis (pilulis gracillimis 0.2–0.5 mm. longis), margine anguste revolutis; petiolo gracili 0.3–0.6 mm. longo; inflorescentia terminali laxa



cymosa 3–5 cm. diametro 6–12-flora; calyce 7–8 mm. longo, tube 4–4.5 mm. diametro basi rotundo sessili, lobis triangularibus acutis erectis ca. 3 mm. longis et 2.5 mm. latis, extus griseis minute villulosis, intus albis dense strigosis; corolla alba infundibuliformi ad 17 mm. longa a basi 3 mm. crassa sursum gradatim expansa, limbo 15–18 mm. diametro, lobis ascendentibus rotundis 5–7 mm. diametro extus sparse inconspicue stipitato-glanduliferis et secus nervum medialem pilos paucos albos adpressos ad 1 mm. longos proferentibus; filamentis attenuatis ca. 8 mm. longis stipitato-glanduliferis nullo modo villulosis ca. 4.5 mm. supra basim corollae affixis apice basim sinuum limbi corollae 1–2 mm. longe superantibus; antheris 3 mm. longis; granulis pollinis 3-colpatis a latere visis transverse ellipticis  $65\ \mu$  latis  $50\ \mu$  altis, desuper visis circularibus vel plus minusve triangularibus  $65\ \mu$  latis; stylo glaberrimo 10–12 mm. longo apice 2–3 mm. profunde bilobato; fructu ignoto.

MEXICO: rocky limestone hillside 1 mile west of Colotlipa, Guerrero, 2700 ft., tree 15 ft. tall with white flowers, June 24, 1953, *Chester M. Rowell, Jr. & H. D. Irby 3545* (TYPE, Arn. Arb.).

An arborescent species with funnelliform corollas, ascending corolla-lobes and non-exserted stamens. Its relatively small, oblanceolate leaves are neither pustulate nor hairy on the upper surface. The plant grows in the same region as *Bourreria spathulata* (Miers) Hemsl. The latter is readily distinguished by having widely spreading corolla-lobes, conspicuously protrudent villulose, as well as glanduliferous filaments, and smaller leaves with few evident veins and a short-strigose, usually pustulate upper leaf-face. The closest relation of *B. Rowellii* is probably *B. Hintonii* Johnston of coastal Guerrero. The latter has scabrous upper leaf-surfaces but otherwise the plant is practically glabrous. Its calyx is narrower and the calyx-lobes more slender and its filaments completely glabrous, bearing neither hairs nor stipitate glands.

### *Tournefortia Romeroi*, sp. nov.

Frutex 2 m. altus velutinus; ramis hornotinis fistulosis ad 0.9 mm. crassis dense velutinis (pilis ca. 1 mm. longis abundantissimis); foliis elliptico-lanceolatis 12–25 cm. longis 5–9 cm. latis, apice graciliter longeque attenuatis, basi acutis in petiolum 10–20 mm. longum 2–3 mm. crassum velutinum attenuatis, margine inconspicue minuteque denticulatis, supra sparse velutinis (pilis ca. 0.5 mm. longis erectis solum in aerolis nervorum crebris secus nervos ipsos carentibus); subtus pallidioribus dense velutinis (pilis ca. 1 mm. longis gracillimis solum secus costam et nervos gestis); nervis laminae folii primariis utroque latere costae 12–15 arcuatis, eis secundariis tertiariisque reticulato-anastomosantibus in facie superiore folii areolas minutas 0.5–1.0 mm. latas numerosissimas circumscribentibus; inflorescentia e axillaribus foliorum superiorum orienti pendula 5–7 cm. longe pedunculata dichotoma, ramis duobus simplicibus 5–10 cm. longis vel eis iterum ramosis; calyce sessili, lobis conspicue inaequalibus gracilli-

mis subulatis supra medium non rariter recurvatis basim versus 0.4–0.6 mm. latis, lobo majore 7–8 mm. longo, minore 4–6 mm. longo; corolla pallide viridi 10–12 mm. longa, extus pilulis 0.1–0.2 mm. longis sparse obsita, intus glaberrima, tubo elongato infra medium 0.5–1.0 mm. crasso, apicem versus crassissimo in faucis 2–3 mm. longos 1.5–2.5 mm. crassos expanso, lobis ascendentibus lanceolatis vel oblongis acuminatis 1.8–2 mm. longis 0.8–1.5 mm. latis; antheris oblongis ca. 0.7 mm. longis supra basim affixis; filamentis perbrevibus 0.1–0.2 mm. longis ca. 1 mm. infra basim loborum corollae insertis; ovario glabro sub anthesi angusto ovoideo ca. 1 mm. longo stylum glabrum 4–6 mm. longum proferenti; stigmatum annulum ca. 0.5 mm. diametro gerenti, apice appendiculam sterilem 0.3–0.5 mm. longam subconicam proferenti; fructu ignoto.

COLOMBIA: La Guayacana (Tumaco), dept. Nariño, shrub 2m. tall, inflorescence pendant, sepals green, corolla pale green, lobes on face pale salmon-color in age, ovary green globose-oblong, June 24, 1951, *R. Romero-Castañeda* 2837 (G); El Diviso, Km. 86 F.C. Tumaco, dept. Nariño, shrub 2 m., inflorescence pendulous; corolla pale green, the lobes pale salmon in age, sepals green, "oreja de macho," July 27, 1952, *R. Romero-Castañeda* 3317 (TYPE, Arn. Arb.).

A very well marked species notable for its velvety indument, the pendulous inflorescence, the very slender and elongate sepals, and the slender elongate corollas. The two collections studied are dark from a very dense velvety indument decidedly brown in color. It is not known if this color is present in the living plant or if it is assumed by the plant in drying.

Associated with this new species from southwestern Colombia, is the name of the collector, Rafael Romero-Castañeda, of the Ministerio de Agricultura, Bogota. Sr. Romero-Castañeda has sent me various lots of Boraginaceae collected during his travels about Colombia. It is fitting that his name should be associated with one of his most attractive discoveries.

### *Tournefortia microcalyx* (R. & P.), comb. nov.

*Heliotropium microcalyx* R. & P. Fl. Peruv. 2: 3, t. 109b (1799).

*Tournefortia obtusiflora* Benth. Bot. Voy. Sulphur 140 (1845).

Over 25 years ago, Contr. Gray Herb. 81: 72 (1928), after study of authentic material, I indicated that the species of Ruiz & Pavon was properly classified as a species of *Tournefortia*, but by some mischance the new name required in transferring it to *Tournefortia* was never published. The plant concerned is a readily recognizable one apparently common in a large area in the province of Lima, Peru. Although the source of the type-collection was originally given as "in Peruviae collibus per Huanuci Provinciam", I have collections of the species only from west of the high mountains. It apparently ranges from the Lima area northward on the Pacific slope into southern Ecuador.

**Heliotropium Ferreyrae**, sp. nov.

Frutex 6–8 dm. altus; ramis numerosis gracillimis 1–2 mm. crassis ascenderet ramosis inconspicue strigulosis (pilis vix abundantibus gracillimis valde adpressis rectis 0.2–0.8 mm. longis); foliis abundantibus non rariter fasciculatis 2–5 cm. longis 1–5 mm. latis, supra medium latioribus deinde deorsum in basim subpetiolatam gradatim longeque attenuatis, apice gradatim attenuatis, supra strigulosis (pilis 0.2–0.5 mm. longis) costa profunde sulcata donatis, subtus pallidis pilis 0.2–1.0 mm. longis vestitis costa prominenti donatis; cymis caulem ramosque terminantibus ebracteatis geminatis ternatisve gracillimis multifloribus 5–25 cm. longis solum ad apicem scorpioideis; floribus numerosis sub anthesi congestis, fructiferis 5–15 mm. distantibus; calyce ad anthesin 2 mm., longo pentifido, lobis inaequalibus anguste lanceolatis tubo corollae subaequilongis; calyce fructifero vix accrescenti 0–1 mm. longe pedicellato; corolla alba 2.3–2.7 mm. longa; tubo corollae subcylindrico 1.5–1.7 mm. longo ca. 1 mm. crasso, extus strigoso, intus secus venas infra lobos corollae positas minute albo-hispidulo alibi glabro; limbo corollae 2–2.2 mm. diametro, lobis recurvatis triangularibus ca. 0.7 mm. longis; sinibus limbi basi truncatis inflexo-plicatis; antheris elongatis haud cohaerentibus subsessilibus 0.8 longis ad 0.2 mm. latis ad 0.8 mm. supra basim corollae basifixis, apice rotundis nec appendiculatas nec pilas evidentis gerentibus; stigmatibus subsessili elongato sursum angustato ad 0.8 mm. longo basi annulo ad 0.25 mm. diametro donato, apice angusto ad 0.15 mm. crasso saepe obscure emarginato; fructu ca. 1.5 mm. alto ca. 2 mm. lato 4-lobato apice obtuso stigmatem sessilem gerente; nuculis 4 dorso convexis et strigosis, ventre angulatis.

PERU (Prov. Piura): 100 km. south of Piura, shrub 6–8 dm. tall, sandy pampa, 250–300 m. alt., fl. white, May 2, 1949, *Ramón Ferreyra 6044* (TYPE, Arn. Arb.).

A species most closely related to *Heliotropium polyanthellum* Johnston of northern Peru but quickly distinguishable from it by having lines of hairs in the corolla-throat and by having a subsessile stigma. In the related species the corolla-throat is glabrous and the stigma is borne on a style 0.2–0.3 mm. long. The proposed species has other characters in its scanty indument, very slender and elongate loosely branched stems, greatly elongating cymes, and small corolla with proportionately shorter tube.

**Coldenia Ferreyrae**, sp. nov.

Frutex prostratus glanduliferus dichotome ramosus; caulibus 1–5 dm. longis nodosis faciliter disarticulatis, internodis 1–5 cm. longis 1–4 mm. crassis juventute hispidulis et stipitato-glanduliferis, maturitate cortice chartacea decidua donatis; foliis ad nodos caulis aggregatis; lamina crassiuscula strigosa vel adpresse hispidulo-villulosa et sparse glandulifera.



elliptica 0.8–1.5 cm. longa 3–5 mm. lata utroque acuta, basi in petiolum gracilem villosum glanduliferum 3–5 mm. longum attenuata, supra utrinque lateribus costae sulcatae nervis 2–4 sulcatis donata, subtus costa et nervis latis prominulis donatis, margine revoluta; floribus glomeratis; calyce sessili 5–6 mm. longo, lobis sub anthesi subulatis villuloso-hispidulis et glanduliferis tubum corollae breviter superantibus, tubo calycis fructiferi evidenter 5-costato, costis prominenter suberoso-encrassatis; corolla alba infundibuliformi glaberrima 9–11 mm. longa, tubo cylindrico ca. 4.5 mm. longo et ca. 1 mm. crasso, limbo 5–7 mm. diametro, lobis ascendentibus obovatis ca. 3 mm. longis 2–2.3 mm. latis; filamentis filiformibus 4–7 mm. longis evidenter exsertis, in faucibus 5–6 mm. supra basim corollae insertis, infra insertionem deorsum secus costam invaginatam tubi corollae 2–3 mm. longe decurrentibus (tubo corollae infra basibus decurrentibus filamentorum nullo modo appendiculato); antheris ca. 1.0 mm. longis; pollinis desuper visis ca.  $33\ \mu$  latis plus minusve trilateralibus, a latere visis quadratis  $33 \times 41\ \mu$  poris 3; stylo filiformi 11–14 mm. longo apicem versus furcato, lobis 0.5–1 mm. longis, stigmatibus minutis; ovulis 4; nuculis saepe 2, 1.3–1.5 mm. longis, dorso alte convexis dense minutissimeque papillatis, ventre planis, margine angulatis sed nullo modo alatis.

PERU: (dept. Arequipa): betw. Nazca and Chala, Km. 545–46, Alt. 200 m., fl. white, Nov. 7, 1947, *R. Ferreyra 2506* (TYPE, Arn. Arb.); vicinity of Camaná, 20–30 m. alt., in sand, fl. white, *Ferreyra 2550* (G); Lomas de Camaná, 180–200 m., sand, fl. white, *Ferreyra 8847* (A); Rio de Lomas, Acaré, 800–900 m. alt., *Weberbauer 5734* (G).

A very well marked species readily distinguished from all other South American congeners by having the lobes of the fruiting calyx conspicuously thickened with corky ribs below the middle. The closest relation of the plant is the habitually similar *Coldenia simulans*, which comes from the same floristic area in coastal southern Peru. This latter species may be distinguished from *C. Ferreyrae* by the lobulate appendages which are well developed inside its corolla-tube, a pair being located about 1 mm. below the attachment of each stamen. These appendages, well developed also in *C. dichotoma*, are absent from the corolla of *C. Ferreyrae*. In all the three species mentioned the inner surface of the corolla-tube is ridged for 1–3 mm. directly below the attachment of each of the stamens. The ridges, although readily mistaken for thickened decurrent bases of the filaments, are actually formed by invagination, each of the ridges on the inside of the tube having a complement in a narrow, elongate depression at the same relative position on the outside of the tube. The vein leading to the stamen passes along the summit of the invaginate ridge but along the ridge the vein is not associated with an appendage. Below the invagination, however, there may be knife-like downwardly elongate appendages close to and paralleling the vein on left and right. In *C. simulans* and *C. dichotoma* the bialate appendage associated with the vein is conspicuously well developed just below the invagination, and is there decidedly lobulate and crisped. In *C. Ferreyrae* the appendages accompanying the veins are

obscure and at best very narrow and sometimes are even absent. Their presence or absence can be determined only by examination of the corolla under very high magnification. They are never enlarged, nor crisped, as is the case in both *C. simulans* and *C. dichotoma*.

The South American species are not separable by marked differences in pollen. The grains from species to species differ only slightly in size and form. In polar profile, though sometimes nearly circular, they tend to be more or less definitely three-sided with the angles broadly rounded. There are three pores. In lateral profile the grains are more or less quadrate in outline and are slightly to very evidently longer than broad. Viewed laterally the polar ends are broadly rounded while the sides are nearly straight and parallel. They measure 30–47  $\mu$  in length along the polar axis and 26–33  $\mu$  broad at the equator. The smallest average size occurs in *C. dichotoma* (26 x 30  $\mu$ ) and the largest in *C. grandiflora* (33 x 47  $\mu$ ). Pollen of the North American species has not been examined. The pollen of the Old World *C. procumbens* L., however, though showing general similarities with the *Coldenia* pollen examined, does differ in a number of notable respects. It has three pores and is also three sided in polar profile, but in lateral view is distinctly elliptic and is very much broader than long, being 25  $\mu$  in length along the polar axis and 33  $\mu$  broad at the equator. Unlike the pollen of the South American species, that of *C. procumbens* has a surface not practically smooth, but one that appears distinctly granulate.

### ***Coldenia simulans*, sp. nov.**

Frutex prostratus glanduliferus dichotomus ramosissimus; caulibus 1–5 dm. longis nodosis faciliter disarticulatis, internodiis 1–5 cm. longis 1–4 mm. crassis, juventate hispidulis et stipitato-glanduliferis, maturitate cortice chartacea decidua donatis; foliis ad nodos caulibus aggregatis; lamina crassiuscula ovato vel lanceo-ovato acuta 7–14 mm. longa 3–5 mm. lata, supra strigosa utrinque lateribus costae nervis 2–3 sulcatis donata, subtus prominenter nervosa villulosa secus costam glandulifera, margine valde revoluta; petiolo 2–4 mm. longo glandulifero; floribus glomeratis; calyce sessili 3–4 mm. longo, lobis lanceolatis acutis villulosis tubo corollae subaequilongis; corolla alba infundibuliformi glabra 4.5–6 mm. longa, lobis ascendentibus obovatis ca. 2 mm. longis et 1 mm. latis, tubo cylindrico ca. 3 mm. longo et 1–1.3 mm. crasso summum ad apicem filamenta proferente infra insertionis filamentorum costis invaginatibus ad 1 mm. longis donato, basibus costarum (i.e. ca. 2 mm. supra basim corollae) appendiculis bialatis lobatis et crispis praedito; filamentis filiformibus inaequalibus 4–5 mm. longis evidenter exsertis 3–3.5 mm. supra basim corollae insertis; antheris 0.8–1.1 mm. longis; stylo ca. 7 mm. longo, apice ca. 1 mm. profunde lineariter bilobato; nuculis 2–2.3 mm. longis 1.0–1.3 mm. latis plano-convexis.

PERU (dept. Arequipa): El Jagüay, Km. 538, fl. white, Aug. 22, 1948, *Rosa Scolnik 1010* (TYPE, Arn. Arb.); Puerto de Lomas, Oct. 3, 1931, *Father Jaffuel 2137* (G); Puerto de Lomas, *Weberbauer 5730* (G).

Closely related to *Coldenia dichotoma* and perhaps only a very well developed geographic variation differing in its small leaves and less evident conspicuously fewer veins. Whereas *C. dichotoma* has been found at various stations along the Peruvian coast from Lima north to Talara. *C. simulans* is known only from a limited area of coastal southern Peru lying just south of the Ica-Arequipa departmental boundary.

The Peruvian species of *Coldenia* all show a preference for sandy soil. Indeed, most of them are restricted to dunes, especially those near the ocean. Although proper ecological conditions appear to be almost continuously present along the length of the Peruvian coast, only one species of *Coldenia* ranges along more than half of it. *Coldenia parviflora* and *C. grandiflora* are known in Peru only from the interior, from sandy places and dunes near the city of Arequipa. *Coldenia conspicua* and *C. litoralis* are known from Peru only from the south coast, from Mollendo southward. *Coldenia Ferreyrae* and *C. simulans* are known only from a short section of coast between Mollendo and Lima. *Coldenia dichotoma* is known only from the Peruvian coast from Lima northward. The most widely distributed species, occurring along the coast and also well back from the coast, and in southern as well as in northern Peru, is *C. paronychioides*. Of the eight species known from Peru, five are endemic to the country: three (*C. grandiflora*, *C. litoralis*, *C. paronychioides*) extend well southward into Chile; and only *C. paronychioides* reaches into Ecuador. Only two, *C. dichotoma* and *C. paronychioides*, occur about Lima and northward. The six other Peruvian species all reach their northern limit further south. The eight species of *Coldenia* known from Peru may be distinguished by the following key:

- Nutlets distinctly plano-convex, with a high rounded back and a broad flat commissural face; stamens usually evidently exerted from the corolla. Corolla blue; nutlets with knife-like lateral margins, known from the vicinity of Arequipa (1800–2200 m. alt.) and south into northern Chile. . . . . *C. grandiflora* Phil.  
 Corolla white or very pale bluish; nutlets with angled but not knife-like margins.  
 Fruiting calyx developing prominent corky-thickened ribs; corolla-tube not appendaged a short distance below the attachment of the filaments; plant of coastal southern Peru, 20–900 m. alt. . . . *C. Ferreyrae*, sp. nov.  
 Fruiting calyx without corky-thickened ribs; corolla-tube bearing a pair of crisped lobulate appendages a short distance below the attachment of each filament.  
 Leaves bearing 4 to 6 well developed veins on each side of the midrib; plant of coastal Peru north of Lima, 0–50 m. alt. . . . .  
 . . . . . *C. dichotoma* (R. & P.) Lehm.  
 Leaves bearing only 2 to 3 veins on either side of midrib; plant of coastal southern Peru. . . . . *C. simulans*, sp. nov.



Nutlets not conspicuously flattened on the ventral (commisural) side, more or less sphaerical or lance-oblong in form, not distinctly plano-convex; stamens included and equal or nearly so.

Attachment-scar narrow, elongate, longitudinal on the lance-oblong nutlets; corolla very small 2.5–3.5 mm. long; ranging from northern Chile to Ecuador, along the coast and in the interior, 0–2300 m. alt. ....

..... *C. paronychioides* Phil.

Attachment-scar small, localized on one side of the nearly sphaerical nutlet; corolla larger, over 7 mm. long.

Corolla 11–16 mm. long; calyx 8–13 mm. long, glanduliferous; nutlets 1.2–1.5 mm. in diameter, with a very prominent bony convex commisural surface; coast of southern Peru (Mollendo, Mejia, Cachendo), 0–1000 m. alt. ....

..... *C. conspicua* Johnston

Corolla 7–9 mm. long; calyx 2.5–5 mm. long, not glanduliferous or only very sparsely so; nutlets 1 mm. or less in diameter, commisure not very prominent.

Leaves lanceolate, largest ones 8–17 mm. long, sharply acute, with 3–5 veins on each side of midrib; region about Arequipa, 2200–3400 m. alt. ....

..... *C. elongata* Rusby

Leaves ovate or elliptic, largest one 5–10 mm. long, usually obtuse, 2–3 veins on each side of the midrib; coast of southern Peru (Mollendo, Mejia, Tacna) and south into Chile where it is the most common and wide-spread species. ....

..... *C. litoralis* Phil.

### ***Onosma brachylinum* (Johnston), comb. nov.**

*Onosma Waddellii* var. *brachylinum* Johnston, Jour. Arn. Arb. 32: 345 (1951).

Plant annual or biennial; stems one to several 1–3 dm. long 1.5–3.5 mm. thick, decumbent to erect, usually ascendingly branched, pungently hispid with spreading hairs 1–3 mm. long; leaves veinless or nearly so, all cauline, numerous, green, usually paler beneath, upper surface in age frequently dotted with discoid hair-bases, hispid with straight stiff erect or ascending hairs 1–3 mm. long; lowest leaves largest and more or less oblanceolate, 3–7 cm. long, 8–13 mm. broad; middle leaves 2–4 cm. long, 4–8 mm. broad, sessile; basal leaves not persisting at flowering time; cymes terminal on the main stem and branches and frequently pedunculate in the upper leaf-axils, frequently forked, at anthesis dense, 1.5–2.5 cm. in diameter, remaining congested even in fruit; calyx 5–8 mm. long, weakly accrescent at maturity, lobes hispid, pedicel 1–3(–5) mm. long; corolla usually pink but sometimes blue or white, 11–13 mm. long, with a short tube ca. 2 mm. thick then expanding into a campanulate throat becoming 5–8 mm. in diameter, outside usually inconspicuously strigulose or hispidulous on and below the lobes, inside glabrous except for the usually villulose annulus; corolla-lobes triangular 1–1.5 mm. long, 2–3 mm. broad, margins revolute; anthers 4.5–6 mm. long, coherent at the base and along the sides to form a tube, affixed ca. 1.5 mm. above the base, included or with only the sterile tip exerted, sterile tip 0.4–0.9 mm. long; filaments 2.5 mm. long, arising 3–4.5 mm. above the corolla-base, decurrent base 2–3 mm. long; annulus very narrow, 0.3 mm. high, villulose lobulate; style

glabrous, commonly exerted 1–2 mm.; nutlets 2–2.5 mm. long olivaceous, somewhat lustrous, sparsely papillate and obscurely rugulose.

TIBET: Kyimpu, Chayul—Charme road, among shrubs on stony hillside in warm valley, 12,000 ft., corolla mostly bright reddish pink, some colored blue, July 26, 1936, *Ludlow & Sherriif* 2440 (BM); Trün, Chayul Chen, on rocky open hillside, dry valley, only one plant seen, corolla pink, 11,500 ft., July 22, 1936, *Ludlow & Sherriif* 2418 (BM); Sanga Chöling, Charme, dry stony scrub-covered slopes facing south, not common, plentiful in certain spots, 11,000 ft., Sept. 18, 1935, *Kingdon-Ward* 12355 and 12355A (BM); Kyimdong Dzong, Tsangpo Valley, fl. white, stony screes in rocky gorge, 11,000 ft., July 14, 1935, *Kingdon-Ward* 11991 (BM); Kharkhung, 12,500 ft., June 23, 1936, *N. Humphreys* 5026 (BM).

This plant was previously known to me only from some collections from the Tibetan valleys north of Mt. Everest. The collections cited above come from regions farther east, from the area north of eastern Bhutan. The species is now known to range along the north side of the Himalaya in southern Tibet between long. 87° and 94° E.

Although probably most closely related to *Onosma Waddellii* Duthie, a species of the dry sands and gravels along the Tsangpo Valley, the present plant is readily distinguished from its relative by its looser, more branching habit, its spreading pungent indument, and its included anthers and short (2–3 mm., not 5–7 mm. long) filaments. It is a plant of stony slopes and hillsides. Its corollas are pink or become blue in age, but never achieve the bright blue which is one of the distinguishing features of *O. Waddellii*.

### **Maharanga bhutanica, sp. nov.**

Planta perennis e radice valida palari 5–10 mm. crassa erumpens; caulibus pluribus 1–2 dm. longis simplicibus ascendentibus 1–2 mm. crassis pilis gracilibus patentibus 2–3 mm. longis rigidulis abundante donatis; foliis firmiusculis costa et nervis evidenter donatis adpresse hispidis (pilis rectis abundantibus 2–4 mm. longis) et praesertim in facie inferiore minute inconspicueque strigosis (pilulis 0.1–0.5 mm. longis), maturitate facie superiore basis pallidas discoideas pilorum notatis; foliis basalibus persistentibus 5–9 cm. longis 1–2 cm. latis utroque acutis; nervis utrinque lateribus costae 3–4 validis assurgentibus in facie superiore sulcatis in facie inferiore prominulis; foliis caulinis parvis lanceolatis 1–3 cm. longis 4–8 mm. latis inferioribus quam superioribus aliquandam majoribus vel plus minusve equalibus; cymis terminalibus densis sub anthesi 2–3 cm. diametro; calyce hispido sub anthesi 4–5 mm. longo fere ad medium lobato, lobis triangularibus acutis; corolla caerulea 9–11 mm. longa, base imma 1.5 mm. crassa, medium versus 4–5 mm. crassa, ore 1–2.5 mm. diametro, extus strigulosis (pilulis 0.1–0.3 mm. longis retrorsis antrorsisque) a fundo sinum usque ad medium tubi 5-sulcata, infra medium tubi costis 5 inflatis et areolis 3 planis ellipticis apice haud invaginatibus ornato, intus solum in annulo fere ad 1 mm. alto villulosa alibi glabra; antheris 4–

4.5 mm. longis basi coherentibus inclusis 1 mm. supra basim affixis, apicibus sterilibus denticulatis ca. 0.8 mm. longis, basibus 4–5 mm. infra sinus corollae positis; filamentis 2–2.5 mm. longis, sursum gradatim attenuatis 3.5–4 mm. supra basim corollae affixis; stylo glabro; nuculis ignotis.

BHUTAN: Chungkar, common on cliff-ledges, 7000 ft. alt., corolla blue, pink when first opening, June 6, 1947, *F. Ludlow, G. Sherriff & H. H. Elliot 12598* (TYPE, Brit. Mus.).

This species is a coarse perennial and has the gross habit of *Maharanga emodi* (Wall.) DC. It works out to the latter species in my key to plants of this relationship, Jour. Arn. Arb. 32: 206 (1951). The Bhutan plant differs from *M. emodi* in being much more abundantly hairy and in having elongate corollas, reduced cauline leaves, and conspicuously veined, more persistent basal leaves. In *M. emodi* the cauline are gradually larger upward along the stem, with the lowest imperfectly developed and those below the cyme largest and best developed. In *M. bhutanica* the cauline leaves are all about equally developed with the lowermost only very slightly larger than the uppermost. The proposed new species is known only from relatively low altitudes in Bhutan, whereas *M. emodi* occurs between 10,000 and 15,000 ft. alt. and ranges from Bhutan to Kumaon.

***Maharanga emodi* (Wall.) DC., var. *stelligera*, var. nov.**

A var. typica differt foliis basalibus in utrinque lateris et foliis caulinis in facie inferiore pilis stellatis abundantibus gestis; pilis majoribus 3–6 mm. longis e centro disciformi pallidi erumpentibus, basi pilulos ca. 1 mm. longos plures radiate dispositos disco pallido marginem versus erumpentes circumdatis.

BHUTAN: Tang Chen, Ritang, corolla blue-violet to purple-blue, lobes bright red or reddish blue, on cliff ledges and on steep open slopes among stones, 12,000 ft., *F. Ludlow & G. Sherriff 3234* (TYPE, Brit. Mus.; ISOTYPE Arn. Arb.).

In this plant the basal leaves are pallid with an appressed villose-hispid indument composed solely of stellate hair-clusters. The cauline leaves, however, are green and their sparse indument contains stellate hair-clusters only on their lower surface. Hair clusters of a similar sort occur in two other species of *Maharanga*, *M. egregia* Johnston and *M. Wallichiana* DC.

***Craniospermum echioides* (Schrenk) Bunge, Heliocarya 10 (1871).**

*Diploloma echioides* Schrenk, Bull. phys.-math. Acad. Petersb. 2: 195 (1844).

*Craniospermum mongolicum* Johnston, Jour. Arn. Arb. 33: 74 (1952).

DZUNGARIA: Ala-tua, 1840, *A. Schrenk* (Paris, ISOTYPE of *D. echioides*).  
MONGOLIA: Daying Gol, *Chaney 195* (G, TYPE of *C. mongolicum*).

I have examined the authentic specimens of *Craniospermum echioides*, from the herbarium of Bunge, now preserved at Paris. It is without any doubt conspecific with the type of *C. mongolicum*. The plant involved



appears to be extremely rare and at present is known only from the two localities cited. These two stations both lie near lat. 45° N. but are separated from west to east by over 1500 kilometers.

Brand, Pflanzenr. Heft 97: 103 (1931), apparently saw no material of *C. echioides*, for he lists the species as a synonym of the very different *C. subvillosum* Lehm. Actually the species is not very closely related to the other species of *Craniospermum* and, if it is not eventually separated from them to form the monotypic genus *Diploloma*, it should be segregated within in *Craniospermum* to form the section *Diploloma*, as Popov, Fl. URSS 19: 535 (1953), has recently done.

The pollen of *C. echioides* is sphaerical and 33–39  $\mu$  in diameter. It bears three broad granular elliptic areas, usually more or less protrudent, equally spaced about the equator. I am unable to distinguish it by size or form from the pollen of other members of the genus. The pollen from the type specimen of *C. mongolicum* is mostly imperfect and not characteristic. It is smaller (at most 25  $\mu$  in diameter) than in other collections but otherwise similar.

### **Hackelia Stewartii, sp. nov.**

Planta herbacea perennis 6–10 dm. alta; caulibus erectis fistulosis basim versus ad 8 mm. crassis, apicem versus ramulos paucos ascendentes florigeros 5–20 cm. longos gerentibus; foliis caulinis lanceolatis; lamina 6–18 cm. longa 2 — 8 cm. lata, basi acuta vel plus minusve obtusa in petiolum 5–35 mm. longum contracta, apice graciliter attenuata, facie inferiore pallidiore villulosa pilulis mollibus 0.1–0.5 mm. longis vix abundantibus vestita, facie superiore viridi scabrella pilulis gracilibus inconspicuis adpressis 0.1–0.6 mm. longis obsita; nervis lateralibus laminae evidentibus, eis in tertia parte inferiore costae orientibus conspicue longissimis fere ad apicem folii attingentibus; cymis solitariis vel geminatis in caulibus et ramulis terminalibus 7–15 cm. longis ebracteatis vel basim versus bracteas saepe solitariis foliatis 1–4 mm. longas gerentibus; calyce pallido dense villuloso, lobis acutis ad anthesin cuneato-lanceolatis 1.5–2.5 mm. longis 0.6–1.0 mm. latis, in statu fructifero plus minusve ovatis ad 3.5 mm. longis et 2 mm. latis; corolla pallide azurea 10–14 mm. diametro, tubo 1.5–2 mm. longo, lobis rotundis patentibus ad 4 mm. diametro; appendiculis faucium exsertis oblongis 1–1.3 mm. longis 0.8–1 mm. latis marginibus lateralibus villosis; nuculis marginatis dorse non rariter inconspicue hispidulis; corpore nuculae 4.5–5 mm. longo 2–3 mm. lato, margine saepe alato, ala 0.3–2 mm. lata appendiculas uniseriatis subulatas glochidiatas 1–3 mm. longas armatas; gynobasi 2.5–3 mm. longa basi ca. 2 mm. crassa; stylo elongato 2–2.5 mm. longo maturitate saepe exserto.

KASHMIR: Rajdhiangan Pass, fl. pale blue, July 19, 1940, *R. R. Stewart 19526* (TYPE, Gray Herb.); trip to Gurais, May–June, 1929, *R. R. Stewart 12955* (G); Sonamarg, 11,000 ft., fl. light blue, July 18, 1928, *R. R. Stewart 12959* (G); Killanmarg, 10,000 ft., Aug. 1926, *R. R. Stewart 8604A* (G); Pahlgam, 10,000

ft., Aug. 8, 1927, *R. R. Stewart 12956* (G); mountains opposite Pahlgam, 11,000 ft., fl. pale blue, Aug. 28, 1945, *R. R. Stewart 21816* (G); Zur Nar above Arie, Liddar Valley, fl. large and dark, usually sky blue, half inch in diameter, Aug. 3, 1945, *R. R. Stewart 21563* (G); 6 mi. south of Karagbal, fir forest, 8000 ft., plant 3 ft. tall, fl. sky blue, Aug. 1, 1936, *W. Koelz 9239* (G).

A readily recognizable species which appears to be most closely related to *Hackelia uncinata*, the most widely distributed member of the genus in the western Himalaya. In gross habit it is intermediate between that of *H. uncinata* and *H. macrophylla*. Both of these latter species range in same general area as that in which *H. Stewartii* is found. The proposed species may be distinguished from the other Himalayan species of the genus by the following key:

Upper leaf-face more or less lustrous, glabrous or nearly so; corolla 10–15 mm. in diameter, white or white with a blue or purple spot between the bases of the lobes; nutlets bearing glochidiate appendages on the dorsal surface as well as on the margin; Kashmir and adjacent Punjab. . . . .  
 . . . . . *Hackelia macrophylla* (Brand) Johnston.

Upper leaf-face with abundant minute appressed hairs, not lustrous; corolla pale to dark blue; nutlets not bearing glochidiate appendages on the dorsum, bearing them only on the margin.

Style elongate, 2–2.5 mm. long; corolla large, 10–14 mm. in diameter, pale blue, faucal appendages longer than broad, 1–1.3 mm. long, ca. 0.8 mm. broad; stem leaves large, broadly lanceolate, 6–18 cm. long, 2–8 cm. broad, lower ones not cordate; Kashmir. . . . . *Hackelia Stewartii*, sp. nov.

Style short, 0.2–0.8 mm. long; corolla usually less than 10 mm. in diameter, faucal appendages usually broader than long, 0.3–0.8 mm. long and 0.6–0.9 mm. broad; stem leaves usually ovate, commonly 6–9 cm. long and 2.5–5 cm. broad.

Calyx usually densely appressed hairy; lowest leaves well developed, usually cordate; cymes becoming loose in fruit; Kashmir to Nepal. . . . .  
 . . . . . *Hackelia uncinata* (Benth.) Fischer.

Calyx and especially the lobes, sparingly strigose or nearly glabrous; lowest leaves small, not cordate; cymes relatively few flowered and dense; Sikkim to Yunnan. . . . . *Hackelia brachytuba* (Diels) Johnson.

**Mertensia Meyeriana** Macbride, Contr. Gray Herb. 48: 52 (1916); Popov, Fl. URSS. 19: 249 (1953).

*Mertensia Popovii* Rubtz. Fl. URSS. 19: 247 and 706 (1953).

The label associated with the type collection of *Mertensia Meyeriana* has the following data "On Chinese territory near Saisansk, so. Siberia, May 20, 1911, *F. N. Meyer* no. 727". When the species was published the geographic data were misread and were given incorrectly as "Zairansk, western Mongolia". A study of the itinerary of Meyer reveals that on May 20, 1911, he was near the Kazakh-Dzungaria boundary, southeast of Lake Zaisan, at about lat. 47° 30' N and long. 85° 00' E., probably at the west end of the Saur Mts. "Saisansk" is an old spelling for the town in East Kazakhstan appearing on recent maps as Zaisan or Zaysan. It is

clear, therefore, that the type of *M. Meyeriana* comes from the region designated in the Flora URSS as the "Dzungaro-Tarbagatai" floristic area, the very area in which *Mertensia Popovii* is endemic. The latter species is said to range, "In montibus Tarbagatai et Saur, satis frequens". Its lengthy description in the Fl. URSS applies perfectly to the type of *M. Meyeriana*.

***Mertensia nemorosa* (DC.), comb. nov.**

*Lithospermum ovalifolium* Decne. in Jacquemont, Voy. Inde Bot. 121, t. 124 (1844).— In humidis nemorum ad Ouri [Uri on Jhelum River], May 4, 1831, Jacquemont.

*Eritrichium nemorosum* A. DC. Prodr. 10: 123 (1846).— Based on *Lithospermum ovalifolium* Decne (1844), not *Eritrichium ovalifolium* DC. (1846).

A Kashmir plant most closely related to *M. racemosa* (Royle) Clarke of Kumaon, Bashahr and Kulu. It differs conspicuously in its blue-purple, rather than white corollas, and its coarser habit. Unlike *M. racemosa* its lower leaves are not subcordate at the base and the herbage usually darkens and becomes more or less chocolate-brown in drying.

The binomial *Mertensia ovalifolia* Brand, Pflanzenr. Heft 97: 199 (1931), was coined by Brand and applied to two very different plants: *Eritrichium ovalifolium* DC. Prodr. 10: 123 (1846), which is a species of *Trigonotis*, and *Eritichium nemorosum* DC. op. cit., our present species of *Mertensia*. In both applications Brand indicated that his binomial was a "nom. nov.". In Index Kewensis, Suppl. 9, *Mertensia ovalifolia* Brand is taken up as based upon *Eritichium ovalifolium* A. DC. This decision associates the name with the species of *Trigonotis* and makes it unavailable for our *Mertensia*.

The name "*Mertensia moltkiioides*" has been applied to the present plant. Indeed, Coventry, Wild Fl. Kashmir 31: 91, t. 46 (1930), has an excellent colored illustration of it under that name. *Mertensia moltkiioides* Clarke, however, is based entirely upon the plant in Royle's Illustrations, which is described as *Myosotis moltkiioides* (on pg. 305) but illustrated, on Plate 73, as *Anchusa moltkiioides*. Royle's plant, from Pir Panjal Pass, must be reexamined. I believe it will be found to represent not the present species, but rather, *Mertensia primuloides* (Decne.) Clarke.

***Mertensia exserta*, nom. nov.**

*Craniosperm parviflorum* Decne. in Jacquemont, Voy. Inde Bot. 126, t. 130 (1844).— Type from the northwest extension of the Pir Panjal Range, from the south side of the pass [i.e. Aliabad or Haji Pir pass] traversed by the road from Punch north to Uri on the Jhelum River, about long. 74° and lat. 34°, collected May 3, 1831 by Jacquemont. Not *Mertensia parviflora* G. Don (1837).

*Moltkia parviflora* (Decne.) Clarke, Fl. Brit. India 4: 174 (1883).



Although it has elongate, much exserted stamens associated with a very reduced corolla, this plant otherwise agrees well with the species representing *Mertensia* in the western Himalayas. Authors, upon the basis of superficial resemblances, have classified this plant in the genera *Craniospermum* and *Moltkia*, but actually it has no immediate relationships with either genus. It is aberrant in *Mertensia* in having elongate, much exserted stamens associated with a reduced corolla, but in all other respects (and especially so in distribution, habit, fruit, and pollen) it shows definite relations with the Himalayan representatives of that genus. It obviously should be classified with the latter plants. I find it surprising that the species has not been transferred to *Mertensia* years ago.

***Mertensia Trollii* (Melch.) comb. nov.**

*Moltkia Trollii* Melch. Notizbl. Bot. Gard. Berlin 15: 115 (1940). — TYPE from Tragbal Pass, Kashmir, *C. Troll* 7028.

*Mertensia Coventryana* S. Clay, The Present-Day Rock Garden, pp. xx and 379, t. 27a (1937). — a provisional name for a cultivated plant; unaccompanied by technical description or Latin diagnosis. The published photograph, plate 27a, was made by B. O. Coventry at Banihal, Kashmir, 9000 ft. alt., May 17, 1929, and is to be associated with the herbarium-specimen, *Coventry 1448*, bearing the same data, which is now preserved at the British Museum.

This species is related to *Mertensia exserta* (= *Moltkia parviflora* Clarke) and confused with it in most herbaria. Both species have stamens conspicuously exserted from the corolla. *Mertensia Trollii* differs from its more common relative in having much larger corollas that have well developed lobes and five invaginate hemispheric appendages in the throat. The corolla lobes of *M. Trollii* are oblong or elliptic and 2–2.5 mm. long. Those of *M. exserta* are more or less triangular and usually 1–1.5 mm. long.

## THE MECHANISM OF CONTROLLED GROWTH OF DWARF APPLE TREES \*

A. G. DICKSON AND EDMUND W. SAMUELS

VARIOUS METHODS have been used to dwarf apple trees and induce earlier fruiting. Standard varieties are budded or grafted on clonal varieties of dwarfing rootstocks. These dwarfing rootstocks have been used for at least several hundred years in Europe, and in recent years they have been introduced into North America. In this country dwarfing interstocks are often used. This method was described by John Rea in England in 1665 as follows: "I have found out another expedient to help them forward, that is by grafting the Cyen of the Paradise apple in a Crab, or other Apple-Stock, close to the ground, with one graft, and when that is grown to the bigness of a finger, graft thereon about eight inches higher, the fruit desired, which will stop the luxurious growth of the Tree, almost as well as if it had been immediately grafted on the forementioned layers, and will cause the Trees to bear sooner, more and better fruits" (Graves, 1950).

The practice of ringing the bark of fruit trees and vines to induce earlier fruiting is an even older art and was described by Virgil and Columella (Louden, 1850). In 1820 Williams described the effects of girdling grape vines as follows: "At the end of July and the beginning of August, I took annular excisions of bark from the trunks of several of my vines, and that the exposed alburnum might be again covered with new bark by the end of autumn, the removed circles were made rather less than a quarter of an inch in width. In every case in which circles of bark were removed, I invariably found that the fruit not only ripened earlier, but the berries were considerably larger than usual, and more highly flavored". The girdling of grape vines is still a standard practice (Weaver, 1955). The girdling of fruit trees, however, has been largely abandoned.

The practice of training the branches of fruit trees in a horizontal position to suppress growth and induce earlier fruiting has long been practiced in Europe. The knotting of the stems of trees by the Japanese to augment the production of miniature ornamental trees is also an ancient art.

A new technique for dwarfing trees has been developed recently, based upon the polarity of phloem or auxin transport (Sax, 1954). This practice involves the removal of a ring of bark from the trunk of a tree and replacing it in an inverted position. The inverted ring of bark is bound tightly with a rubber band until it is united with the wood. Because of the inverted polarity, the ring of bark acts as a phloem block, inhibiting the flow of plant nutrients to the roots of the tree.

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The physiological mechanism of the dwarfing effect of girdling, of dwarfing rootstocks and interstocks and of bending the branches of a tree was known by Thomas Andrew Knight nearly a hundred and fifty years ago. According to Knight (1822) the nutrient sap elaborated in the leaves passes down the bark, and when checked by girdling the bark, "the repulsion of the descending fluid therefore accounts . . . for the increased produce of blossoms, and the more rapid growth of the fruit upon the decorticated branch. . . ." The effect of the dwarfing rootstock was attributed by Knight (1822) to the obstruction of the descending sap at the graft union. He observed that "the effects produced, both upon the growth and produce of the tree, are similar to those which occur when the descent of sap is impeded by a ligature, or by the destruction of a circle of bark". In 1803 Knight, in discussing the fruiting of horizontal branches, observed that it was "by no means improbable, that the formation of blossoms may, in many instances, arise from the diminished action of the returning system in the horizontal or pendent branch". Thus, all of these mechanisms of dwarfing and induction of earlier fruiting are attributed to the checking of the flow of nutrient sap to the roots, which checks vegetative growth, and the accumulation of the nutrient sap in the top of the tree, which promotes flowering and fruiting.

The advent of radioactive tracers has made possible a more critical analysis of the physiological mechanism of dwarfing trees by bark inversion and dwarfing rootstocks and interstocks. In 1954 a series of experiments were started to trace phloem transport in dwarf apple trees with the aid of radioactive phosphorus.

The radioactive phosphorus was carried in a solution of  $\text{KH}_2\text{PO}_4$  which had a radioactivity of about 1 mc. per ml. From 0.35 to 1.0 ml. of the solution was poured into a small glass tube which had been sealed at the lower end around the cut petiole of a leaf. One ml. of the solution was absorbed in from 35 to 45 minutes. Tests with a Geiger counter showed that the radioactive phosphorus reached the base of the tree, a distance of 1.5 to 2.0 feet, in from 4 to 6 hours, and that the accumulation of the isotope was well defined in about 3 days.

The first experiment was done on a Baldwin apple tree three years old which had been dwarfed by inverting two rings of bark the previous year. The isotope was fed through the petiole of a leaf on the lowest lateral branch. The speed of transport to the end of the lateral branch indicated that the isotope entered the xylem and passed up the stem in the transpiration stream. After its incorporation in the leaves into the organic nutrients it passed down the phloem. The distribution of the isotope three days after application is shown in figure 1. There was a gradual increase in radioactivity from the lateral branch down the trunk. The counts reached a maximum of 126,000 per minute in the inverted bark. Below the inverted rings of bark the count was greatly reduced to little more than 15,000 counts per minute. Obviously the downward flow of the isotope, and presumably of the organic nutrients was greatly retarded by the inverted rings of bark. As a result there was an accumulation of the isotope



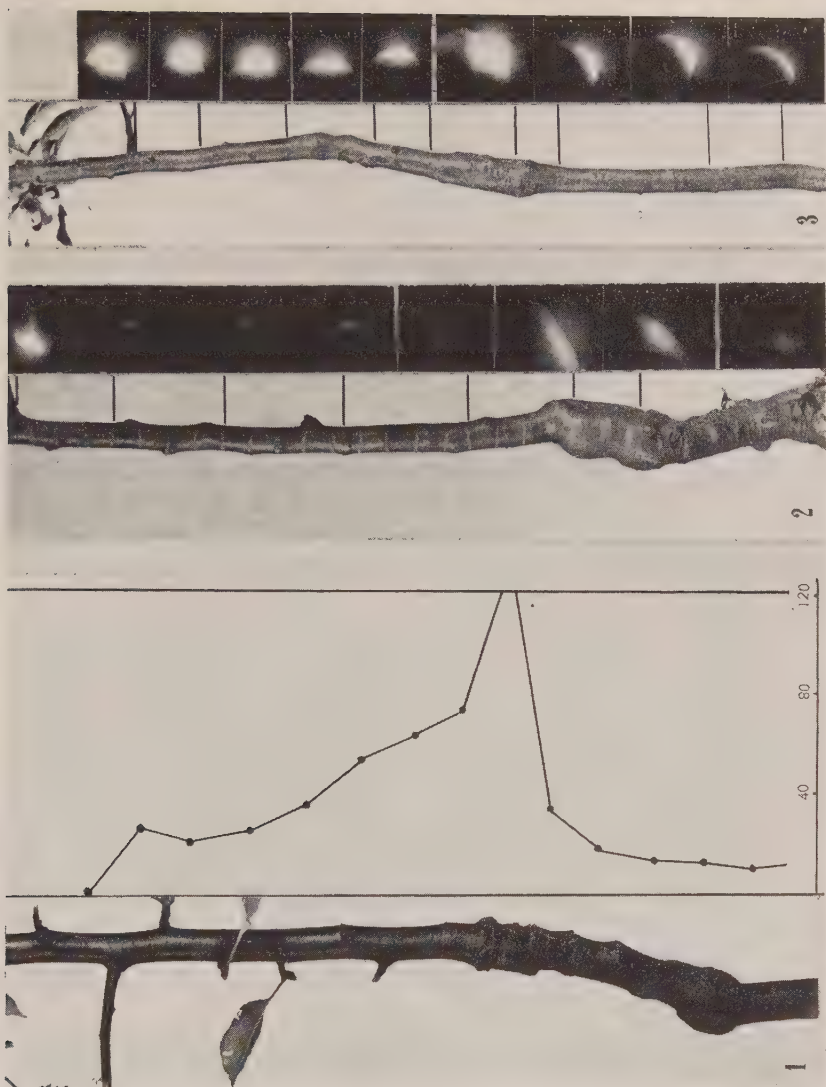


FIG. 1. The distribution of radioactive phosphorus in the trunk of an apple tree, which had been dwarfed by inverting two rings of bark, was measured with a Geiger counter three days after the application of the isotope. Note the great concentration of the isotope at the inverted ring of bark, and the great reduction in concentration below the bark inversion. In all cases the isotope was fed through a leaf petiole on the lowest lateral branch. (Measured in thousands of counts per minute.)

FIG. 2. The distribution of the isotope in the stem of an apple tree on a Malling IX interstock is shown by autoradiographs of transverse stem sections cut three days after the application of the isotope. Note the concentration of the isotope in the dwarfing interstock.

FIG. 3. The distribution of the isotope in the stem of an apple tree with a Clark's Dwarf interstock is shown by autoradiographs of stem sections cut seven days after the application of the isotope. The isotope is concentrated in the dwarfing interstock.

for a considerable distance above the bark inversions and phloem transport to the roots was reduced.

The tracing of the flow of the isotope down the trunks of young apple trees dwarfed by dwarfing interstocks presented a more difficult problem. The dwarfing interstocks have a relatively thick bark and the greater distance between the phloem and the outer surface of the bark reduces the beta radiation reaching the Geiger counter. In order to avoid the discrepancy caused by the difference in thickness of the bark of the Malling IX and Clark's Dwarf interstocks and the rootstock and scion varieties, the concentration of the isotope was measured by autoradiographs of transverse sections of the trunk of the tree. The trunks of the young trees were cut in transverse sections about 5 mm. thick and numbered serially from top to bottom. Sections from various parts of the stem were mounted on a cellophane sheet and the cellophane was drawn tightly over a glass plate. Ansco isopan film, emulsion side down, was placed on the cellophane and the stem sections were exposed for 15–20 hours. All sections of a tree were exposed, developed and printed together to insure uniformity of treatment.

The isotope was fed into the end of a severed petiole of a five-year-old McIntosh apple tree which had been dwarfed by a Malling IX interstock on a *Malus sikkimensis* rootstock. Three days later, on June 14th, the trunk of the tree was cut into serial sections and autoradiographs of selected sections were made on June 16–17. There was a rather high concentration of the isotope at the junction of the lateral branch with the main trunk of the tree, but only very low concentrations in the lower trunk of the tree above and below the interstock. The Malling IX interstock, however, showed a great concentration of the isotope, as shown in figure 2.

In the third experiment the isotope was fed into a petiole on the lowest lateral branch of a three-year-old Starking apple tree on a Clark Dwarf interstock with a Virginia Crab rootstock. Stem sections were made seven days later and the autoradiographs were made with a 17 hour exposure. The results are shown in figure 3.

The high concentration of the isotope at the junction of the lateral branch with the trunk of the tree was again evident. Considerable radioactivity was found between the junction of the lateral branch and the Clark's Dwarf interstock, followed by a considerable increase in the interstock and a reduction below the interstock. Autoradiographs of four sections through the interstock were obtained and all showed a marked increase in radioactivity with the greatest concentration near the bottom of the interstock. It is evident that both Malling IX and Clark's Dwarf interstocks accumulate the isotope, and presumably the organic nutrients, carried down the phloem.

The fourth experiment was done with a four-year-old McIntosh tree which had been dwarfed by tying a knot in the *M. sargentii* interstock. In 1955 five such trees flowered and fruited heavily while the five adjacent control trees, in which the interstock was not knotted, bore no flowers. The isotope was applied in the usual manner and the stem sectioned three days

later. Autoradiographs showed a great concentration of the isotope at the junction of the lateral branch with the main stem, and a secondary and less marked concentration in the stem just above the knot and at the lower end of the knot before the stem began its upward turn. There was little radioactivity in the upper side of the loop or in the stem below the knot. Although the results were not as striking as those obtained with trees dwarfed by bark inversion or dwarfing interstock, there was some indication that the knot had restricted phloem transport.

The dwarfing effect of inverting a ring of bark appears to be caused by the checking of phloem transport, but the mechanism may involve other factors. Since phloem transport is not polar, the inversion of a ring of bark should not interfere with the pressure flow mechanism (Bonner and Galston, 1952). Auxin transport is, however, normally polar and its basipetal movement would be prevented by inverting a ring of bark. Inhibition of auxin flow is indicated by the fact that the dormant buds below the inversion are stimulated into active growth and new growth continues during the summer even when the first sucker branches are removed. Some release of dormancy is effected by simply removing a ring of bark and replacing it in the normal position, but this effect is much more temporary.

The deficiency of auxin in the inverted bark may inhibit phloem transport directly, or indirectly, by the inhibition of cambial activity and growth of the stem. It is known that the inversion of a ring of bark suppresses the growth of the stem in the inverted region, and in a rapidly growing tree there is a great overgrowth of the stem above the inversion.

The dwarfing effect of the dwarfing interstocks also appears to be associated with the retardation of phloem transport. Since the dwarfing interstocks are normally polarized there should be no blocking of the basipetal movement of the auxin. In contrast to the inverted ring of bark the dwarfing interstock grows more rapidly than either the stem of the rootstock or the stem of the scion variety. Perhaps both phloem and auxin transport is retarded in the dwarfing interstock. It may be of some significance that the most effective dwarfing interstocks are varieties which are natural dwarfs when grown on their own roots.

The dwarfing effects of girdling the bark, the use of dwarfing rootstocks and interstocks and the inversion of a ring of bark on the trunk of the tree appear to be associated with the retardation of phloem transport, but dwarfing effects may also be caused by other factors. Peach trees dwarfed by budding them on *Prunus tomentosa* rootstocks show no retardation of the isotope at or below the graft union, nor is there any overgrowth of the dwarfing rootstock as is found with dwarfing Malling apple rootstocks. Even in certain graft combinations of apple varieties the dwarfing effect is not due entirely to the graft union or to the stem of the rootstock (Sax, 1954).

The organic nutrients accumulated at, or above, the phloem block may diffuse into the xylem and be carried by the transpiration stream to the branches where they are used in the production of fruit, as was suggested by Knight in 1820. There is amply experimental evidence to show that



nutrient may pass from phloem to xylem or from xylem to phloem (Crafts, 1951). Colwell (1942) found that radioactive phosphorus applied to the leaf will move down the stem to, but not beyond, a deleted ring of bark, and that immediately above the ring the isotope is found in the xylem as well as the phloem. Greene (1937) obtained a higher starch and sugar content of spurs on ringed branches of Grimes Golden apples than was found on the control branches. Leonard (1938) found that the leaves of an apple variety grown on a Malling IX dwarfing rootstock had a higher content of soluble carbohydrates than those of the same variety of apple grown on a standard rootstock. Stanley Burg in 1954 (unpublished data) found that within a week after the inversion of a ring of bark on the trunk of a maple tree the carbohydrate content of the leaves was greatly increased. Thus the phloem blocks not only check the flow of organic nutrients to the roots, but also increase the organic nutrients of the leaves.

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#### SUMMARY

Apple trees may be dwarfed and induced to fruit earlier by grafting them on a dwarfing rootstock or interstock, or by inverting a ring of bark on the trunk of the tree. The mechanism of these dwarfing effects was

studied with the aid of radioactive tracers. Radioactive tracers were fed through the petioles of the leaves of the lateral branches of young trees. Several days later the distribution of the isotope in the trunk of the tree was determined with a Geiger counter and by autoradiographs of transverse stem sections. The great concentration of the isotope in the dwarfing interstock or in the inverted ring of bark indicates that the dwarfing effect may be caused by checking the flow of organic nutrients to the roots, but the mechanisms involved may be indirect and diverse.

## A RUST ON WOODWARDIA FIMBRIATA

J. H. FAULL

THREE RUSTS have been described on chain ferns; a fourth is recorded as having a chain fern added to its list of hosts. They are: *Uredinopsis Arthuri* Faull II<sup>1</sup>, II<sup>2</sup>, III on *Woodwardia virginica* (L.) Sm.; *U. Arthuri* var. *maculata* Faull II<sup>1</sup>, II<sup>2</sup>, III on *W. areolata* (L.) Moore; *Milesia Tobinagai* (Hirat.) Faull II on *W. japonica* Sm. (described as *Milesina Tobinagai* by Hiratsuka in Journ. Jap. Bot. 12: 271, 1936); and *Hyalop-sora Polypodii* (Pers.) Magnus on *W. orientalis* Sw. *Uredinopsis Arthuri* is reported from the eastern part of North America and not elsewhere; it is recorded from Alabama to Quebec and from Bermuda to Indiana and Michigan. *Uredinopsis Arthuri* var. *maculata* is likewise known to occur in the eastern part of North America only, but in a much narrower range; it is recorded from Alabama to Maine. *Milesia Tobinagai* is from Japan; it was recorded and described from material collected on the island of Kiushû. *Hyalop-sora Polypodii* on *W. orientalis* is reported from Japan; it, too, was recorded from the island of Kiushû. Besides these four there is also an unreported species; that one is on *W. fimbriata* Sm. in California. It is recorded and described below.

Before doing so, however, I should say that I have been reluctant to describe it as a new species. That is so because the urediospores (the only spores so far observed) are like those of *Milesia polypodophila* (Bell) Faull as to size, form, and the not uncommon habit of branching at or near their apices. Of course this rust may be *M. polypodophila*; but many facts have yet to be determined before the answer can be given. Thus: *M. polypodophila* has been reported from eastern North America only; as for its fern hosts there it has been reported only on *Polypodium virginianum*; its alternate host is a conifer, but the loose-broom effect on it is unique; besides that, spermogonia and peridermia are not produced until three years after its infection; it is the only known *Milesia* characterized by such a phenomenon; moreover, its spermogonia are distinctive as to size, length of period of development, abundance of spermatia and length of period of spermatial discharge. So, I have deemed it best to regard this rust on *W. fimbriata* a distinct species pending determination of all its essential features.

***Milesia acuta* Faull, sp. nov., II.**

Spermogonia et aecia ignota. Uredia hypophylla, epidermide tecta, pustulata, rotundata, 0.15–0.5 mm. diam., peridio ex cellulis hyalinis composito cincta; urediosporae fusiformi-obovatae vel fusiformes, acutae



vel acuminatae, subsessiles, hyalinae,  $12-19 \times 32-62 \mu$ , plus minusve circa  $16 \times 51 \mu$ ; paries sporae hyalinus, levis, tenuis. Telia ignota.

Hab. in foliis *Woodwardiae fimbriatae* in California.

O and I. Spermogonia and aecia unknown.

II. Uredia hypophyllous, subepidermal, on discolored areas of indefinite extent, pustular, round, 0.15–0.5 mm. in diameter; peridium hemispheric, peridial cells isodiametrically to irregularly polygonal,  $5-11 \times 5-14 \mu$ , with walls about  $1 \mu$  thick; urediospores hyaline, abundant, extruded in tendrils or masses, very short-stalked, fusiform-obovate or fusiform, acute or acuminate at the apex, occasionally forked or branched at or near the apex, narrowed below,  $12-19 \times 32-62 \mu$ , averaging about  $16 \times 51 \mu$ , wall of spore thin, about  $1 \mu$  thick, smooth, with 4 to 6 germ pores in pairs towards poles or at equator.

III. Telia unknown.

#### HOSTS AND DISTRIBUTION:

O and I. Unknown.

II. *Woodwardia fimbriata* Sm., in California.

III. Unknown.

TYPE LOCALITY: Mt. Tamalpais, Marin County, California. II.

ILLUSTRATIONS: Text-figure 1.

SPECIMENS EXAMINED. —

CALIFORNIA: Mt. Tamalpais, Marin Co., March 31, 1926, *H. E. Parks*; TYPE. — Mt. Tamalpais, May 30, 1935, *L. Bonar*. — Big Sur, Monterey Co., August 14, 1937, *L. Bonar*. — Darlingtonia, Del Norte Co., Feb. 22, 1942, *H. E. Parks*.

The materials studied were all sent by Professor Lee Bonar; too, the specimens of the last lot were sent at the request of Mr. H. E. Parks. Included with this last lot were three microscopic slides of microtome sections made from a part of the collection. They show that the stoma of a uredium is directly under a leaf stoma; also that the opening is encircled by sharp-pointed peridial cells.

On some of the packets there is written "*Hyalopsora Woodwardiae* Jackson, n. sp." This is a *nomen nudum et ineditum*.

Examination of an abundance of urediospores from the type of *Milesia Tobinagai* shows that they are stout and that they are rounded at their apices. They measure  $12-19 \times 19-35 \mu$ , and they average about  $17 \times 25 \mu$ . A good description is given by Hiratsuka in his "A Monograph of the Pucciniastreae", p. 157–8, 1936. There is no likelihood of confusion between *M. Tobinagai* and *M. acuta*.

*Woodwardia fimbriata*, the one recognized host of *Milesia acuta*, extends northward from California into British Columbia. It has passed under the names *W. radicans*, *W. spinulosa* and *W. Chamissoi*. What the coniferous generic host is and what the comparative effects on its species are, remain for experimentation.

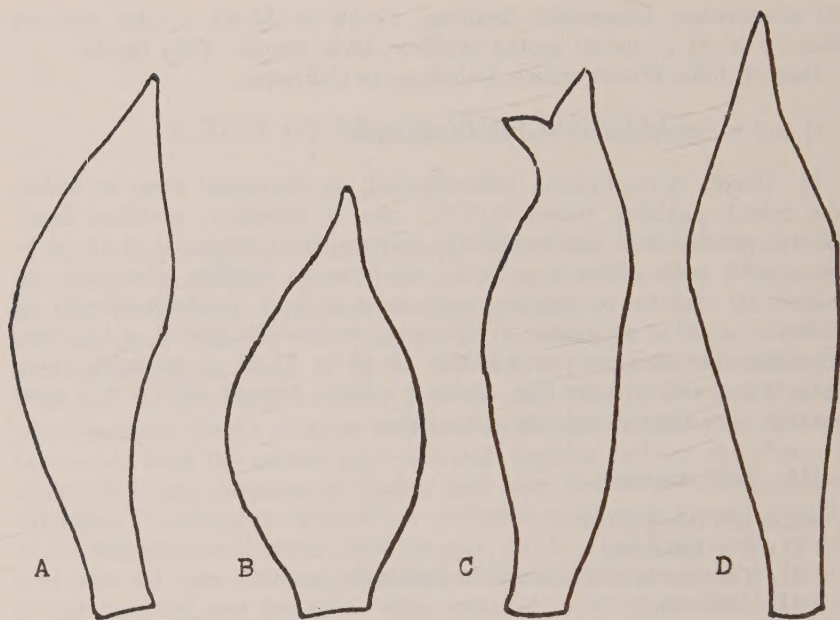


FIG. 1. *Milesia acuta*, sp. nov. Outlines of four urediospores from same microscopic mount. The one at the extreme left is about average size —  $16 \times 51 \mu$ .